Generic Delimitation and Macroevolutionary Studies in Danthonioideae (Poaceae), with Emphasis on the Wallaby Grasses, *Rytidosperma* Steud. s.l.

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For my parents, Pauline and David, with love

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Zusammenfassung

Ein Hauptziel von evolutionsbiologischer und ökologischer Forschung ist die biologische Vielfalt zu verstehen. Die systematische Biologie ist immer in der vordersten Reihe dieser Forschung gewesen and spielt eine wichtiger Rolle in der Dokumentation und Klassifikation von beobachteten Diversitätsmustern und in der Analyse von derer Herkunft. In den letzten Jahren ist die molekulare Phylogenetik ein wichtiger Teil dieser Studien geworden. Dies brachte nicht nur neue Methoden für phylogenetische Rekonstruktionen, die ein besseres Verständnis über Verwandtschaften und Klassifikationen brachten, sondern gaben auch einen neuen Rahmen für vergleichende Studien der Makroevolution vor.

Diese Doktorarbeit liegt im Zentrum solcher Studien und ist ein Beitrag an unser wachsendes Verständnis der Vielfalt in der Natur und insbesondere von Gräsern (Poaceae). Gräser sind schwierig zu klassifizieren. Dies liegt einerseits an ihrer reduzierten Morphologie – die an Windbestäubung angepasst ist – und anderseits an Prozessen wie Hybridisation, die häufig in Gräsern vorkommen, und die die Bestimmung von evolutionshistorischen Mustern erschweren. Gräser kommen mit über 11,000 Arten auf allen Kontinenten (ausser der Antarktis) vor und umfassen einige der ökologisch, ökonomisch und für die Ernährung wichtigsten Arten. Diese Arbeit wird ein besseres Verständnis ihrer Phylogenie und eine verbesserte Klassifikation bringen, sowie wichtige Fortschritte für viele grundlegende und angewandte Forschungsprogramme.

Das Ziel dieser Arbeit wird anhand von 3 Fragen spezifiziert, die offene Fragen zur Phylogenie und der Klassifikation auf Gattungsebene der Gräser beantworten – im Generellen aber auch eine Unterfamilie der Gräser (Danthonioideae: Poaceae): 1) Hinsichtlich der optimalen Gattungsgrössen, führen Veränderungen der Daten oder der Konzepte über die Zeit zu Änderungen der vorherrschenden Gattungsgrösse? 2) Wie wird die Variation der ca. 100 Arten der Gattung *Rytidosperma* und verwandter Grassgattungen am besten in einer Klassifikation auf Gattungsebene organisiert? 3) Was sind die evolutionären Konsequenzen verlorener, ökologisch wichtiger Merkmale und wie hilft die Untersuchung dieser Konsequenzen die Ursachen für die Variation der Danthonioideae-Arten zu erklären?

Frage 1 untersucht, wie sich die Grösse von Pflanzengattungen im Laufe der Zeit verändert haben (Kapitel 1). Historische Literatur und eine Metaanalyse empirischer Studien der letzten 10 Jahre dient als Informationsquelle, um zu untersuchen, ob Änderungen der Konzepte oder der Daten die „bevorzugte“ Gattungsgrösse beeinflussten. Die Resultate zeigen dass Veränderungen in Konzepten zu Änderungen der Gattungsgrössen führen und dass der aktuelle Trend grössere Gattungen zu beschreiben von Studien mit breiterer Abgrenzung stammen und nicht von der Aufnahme molekularer Daten. Mit diesen Resultaten im Hintergrund analysiere ich umfangreiche morphologische- und molekulare Datensätze mit einer Reihe phylogenetischer, kladistischer and klassisch-statistischer Methoden um Frage 2 zu beantworten. Ich stelle eine phylogenetische Hypothese für *Rytidosperma* und verwandter Gattungen vor (Kapitel 2). Obwohl diese Hypothese nur auf Plastidendaten basiert, enthalten diese ein signifikantes, phylogenetisches Signal welches durch morphologische, ökologische und biogeographische Daten gestützt wird. Die Analyse dieser Daten in einem phylogenetischen Kontext zeigt, dass Merkmale der Lemma, der Karyopse und der Palea konservativ sind und dass diese für die Diagnose von *Rytidosperma* s.l. benutzt werden können. Dies ist konsistent mit einigen früheren taxonomischen Bearbeitungen dieser Gruppe. Die Analyse zeigt auch ein biogeographisches Muster das mit dem Muster einiger anderer Angiospermengruppen der Südhemisphäre übereinstimmt. Zusammen unterstützen diese Resultate die Benutzung der Hauptgruppen als Richtlinie für eine Revision der Gattungsklassifikation. Ich schlage vor, dass die Anzahl Gattungen in der Gruppe von

sieben auf drei reduziert wird: *Austrodanthonia*, *Notodanthonia* und *Joycea* werden mit *Rytidosperma* synonymisiert *Tribolium* wird breiter, um die meisten Arten von *Karroochloa* zu umfassen und eine Art von *Karroochloa* wird in die Gattung *Schismus* überführt. Um Frage 3 zu beantworten analysiere ich die Evolution der Granne in Danthonioideae in einem phylogenetischen Kontext (Anzahl erworbener und verlorener Merkmale), ich beurteile die Persistenz der Abstammungslinien ohne Grannen, ich beurteile, ob die Evolution der Granne mit der Evolution anderer Merkmale korreliert ist (hier: Lebensgeschichte) und ob die Präsenz oder die Absenz von Grannen mit anderen Merkmalen der Diasporen verbunden ist (Kapitel 3). Meine Resultate deuten an, dass die Granne die sichtbare Komponente eines ‚Eingrabungssyndromes' ist. Ein Extrem dieses Syndromes zeigt sich beim aktiven Eingraben der Grannen mit Hilfe von hygroskopischer Aktivität. Das andere Extrem bringt Modifikation vieler anderer Merkmale mit sich, samt der Reduktion oder dem Verlust der Granne, welche zusammengenommen ein zufälliges Eingraben optimiert. Im evolutionären Zusammenhang haben die Abstammungslinien ohne Grannen generell eine geringere Vielfalt und Beständigkeit. Die Optimierung an zufälliges Eingraben als Teil einer ökologische Änderung die auch eine Änderung in der Lebensgeschichte nach sich zieht, erklärt die Persistenz einiger grannelosen Abstammungslinien, obwohl diese Linien ein ökologisch sehr wichtiges Merkmal verloren haben.

Mit den hier vorgestellten Thesen werden viele neue Fragen aufgeworfen. Zum Beispiel: Welches waren die ökologischen und biogeographischen Hauptfaktoren die zur Evolution von Rytidosperma in Australasien und Südamerika führten? Wie alt sind die einzelnen Arten, besonders landwirtschaftlich genutzten, und was sind ihre biogeographischen Ursprünge? Können die zwei ‚Extreme' des ‚Eingrabungssyndroms' experimentell an verschiedene Erdtypen demonstriert werden? Unter welchen Umständen bringt das aktive Eingraben der Diasporen einen echten Vorteil und unter welchen Umstände ist es überflüssig und kann verloren gehen? Schliesslich stellt sich die Frage, ob sich (Pflanzen-) Systematiker eines Tages betreffend der Klassifikation von Gattungen einig werden. Wenn nicht, was wären die Konsequenzen für vergleichende Studien der Evolution, der Ökologie und im Naturschutz?

Synopsis

One of the major goals of much evolutionary and ecological research is to understand variation in nature known as 'biodiversity'. Systematic Biology has always been at the forefront of this field and plays the important role of documenting and classifying observed patterns of variation and in analysing how they may have originated. In recent years, the field of molecular phylogenetics has been incorporated into systematics research. This has brought with it not only an independent means of objective phylogeny reconstruction that provides new information about relationship that can be incorporated into classifications, but also a framework for carrying out comparative studies in macroevolution.

This thesis lies at the heart of such studies and is a contribution to our growing understanding of the diversity of nature, in particular of the grasses (Poaceae). Grasses are a challenging group to classify. This is in part attributable to their reduced floral morphology – optimised for wind pollination – and in part to their propensity to engage in processes, e.g. hybridisation, that complicate tracing their evolutionary history. Nevertheless, with over 11,000 described species, widely distributed on all continents but Antarctica, some of which are arguably the most ecologically, economically and nutritionally important species known to man, increased understanding of the phylogeny and improved classification of grasses provides important progress for a range of basic and applied research programmes.

To fill some of the gaps in current hypotheses of grass phylogeny and to address classification at the generic level, in general and in one of the subfamilies of grasses (Danthonioideae: Poaceae), the aim of the work presented here was to address the following three questions. 1) With regard to how optimal generic limits are best drawn, what drives changes in prevailing genus size over time; changes in data or changes in concept? 2) How is the variation of the ca. 100 species in *Rytidosperma* and allied grass genera best expressed as a generic classification? 3) What are the evolutionary consequences of losing ecologically important structures and how does an analysis of these consequences help to elucidate what underlies some of the variation among the species of Danthonioideae?

I address question 1 by investigating how sizes of plant genera have changed over time and use information gathered in an extensive review of the historical literature and a meta-analysis of empirical studies on generic delimitation published in the past decade, to investigate whether changes in the concept or in data drive changes in 'preferred' genus sizes (Chapter 1). My results show that shifts in generic concepts drive changes in overall genus sizes, that the current trend toward recognising larger genera is a result of a return to study on a broad scale, rather than incorporation of molecular data. With this in mind and using a range of phylogenetic, cladistic and classical statistics analytical tools, I analyse large and comprehensive sets of both morphological and molecular (nucleotide sequence) data to address question 2. I present a phylogenetic hypothesis of *Rytidosperma* and allied genera. Despite being based on plastid data alone it contains a phylogenetic signal that is significantly supported from morphological, ecological and distribution data (Chapter 2). Analysed in a phylogenetic context, these data reveal conservatism in characters of the lemma, callus, palea and caryopsis that can be used to diagnose *Rytidosperma* sensu lato, consistent with some previous taxonomic treatments of this group. They also reveal biogeographic patterns consistent with those identified in other austral angiosperm groups. Together, these findings support using the circumscription of the major clades as a guideline for a revision of the generic classification. I propose reduction the number of genera in this clade from seven to three: *Austrodanthonia*, *Notodanthonia* and *Joycea* are synonymised with *Rytidosperma* and *Tribolium* is expanded to include most of the species of *Karroochloa*, with one species of *Karroochloa* being transferred to *Schismus*. To address question 3 I analyse the evolution of awns in Danthonioideae in a phylogenetic context (number of gains

and losses), assess whether awnless lineages persist and diversify, whether awn evolution is correlated with the evolution of other traits (here: life history) and whether the presence or absence of an awn is associated with variation in other diaspore traits (e.g. lemma and callus indumentum) (Chapter 3). My findings suggest that the awn represents the visible constituent of a burial syndrome. One of the extremes of this syndrome confers active burial driven by hygroscopic activity of the awn. The other extreme involves modification of several morphological characters, including reduction or complete loss of the awn, which together increase efficiency of stochastic burial. In an evolutionary context, most lineages in which awn loss has occurred diversify little and do not persist. Optimisation toward stochastic burial as part of an ecological shift that also involves a shift in life history, explains evolutionary persistence of a few awnless lineages, despite their having lost this ecologically important trait.

The theses put forward here raise a suite of further questions. What, for example, were the detailed ecological and geographical drivers of the evolution of *Rytidosperma* in Australasia and South America likely to have been? What is the age and biogeographical origin of the individual extant species, with particular reference to those with agricultural importance? Can the different functions of the two extremes of the 'burial syndrome' proposed here be demonstrated experimentally on different soil types? What, in grasses and vascular plants in general, are the circumstances under which active diaspore burial is a real advantage and the circumstances under which it is redundant and can be lost? Finally, I wonder whether there will ever be true consensus among (plant) systematists regarding how best to delimit genera. If not, what are the consequences for comparative approaches to evolution, ecology and conservation studies?

Introduction

The natural world has long been a source of fascination and discovery. In fact, our desire to document, describe and classify nature goes back further than science itself. Here I contribute to our growing knowledge about and understanding of the diversity of nature by presenting a thesis on how variation in *Rytidosperma* and allied grass genera is best classified, what the conceptual underpinning to support this classification is and how some traits may have influenced evolution of this variation. As such, my thesis is about patterns in nature and their evolution. More specifically it encompasses molecular phylogenetics, generic delimitation, cladistic analysis of morphological characters, character optimisation and trait evolution, comparative macroevolution and philosophy of systematics. Not all these elements were part of systematics studies historically, however, and the production of classifications from which evolutionary insight can be read is a fairly recent development of systematics research.

Early classifications were accounts of medicinal plants published as 'herbals' in ancient Greece or China (Arber 1938; Bartlett 1940). With time, and as more organisms were discovered, classifications became more scientific, with leading figures of the eighteenth century, such as Tournefort, Linnaeus and Jussieu, applying rigorous and consistent rules to aid production of clear classifications based on outstanding characters of the organisms they studied (Stearn 1959; Stafleu 1971; Atran 1990; Stevens 1994). As the number of people classifying nature and number of described taxa increased, so did disagreement among systematists (Stevens 1997), disagreement which became manifest as constantly changing classifications. To combat this, and to incorporate novel scientific insight, systematists have often sought new ways of producing classifications. Perhaps one of the most important developments occurred in the mid twentieth century, when Fisher's (1930) genetical theory, Mendelian genetics (Mendel 1866) and Darwinian natural selection (Darwin 1859) were incorporated into taxonomy to give rise to the 'new systematics' (Huxley 1940). The aims of this new, expanded discipline were to discover the products of evolution, with particular reference to species and subspecific groupings (Huxley 1942; Mayr 1942). To achieve this, systematics came to incorporate fields such as genetics, cytology and ecology. While these disciplines shed new light on the nature of diversity and provided new levels of variation along which to delimit groups, these developments were confined to the lower taxonomic ranks and did not provide a solution for generating stable classifications. In the 1960s phenetics rose as a discipline with the aim to produce classifications that were maximally predictive and generally useful (Sokal and Sneath 1963; Gilmour and Walters 1964; Stevens 1984). During the same time, there was a growing notion that the most stable classifications are those in which the units of classification have a real connection, most appropriately a historical one (Hennig 1966; Kornet 1994) that denotes shared ancestry (Bremer and Wanntorp 1978; Funk and Stuessy 1978; Backlund and Bremer 1998).

Incorporation of information on historical relationships into classifications has gained pace in recent decades and has used evidence of shared ancestry as a baseline for delimiting groups. While the idea that classifications should reflect phylogeny is not new, previous attempts to incorporate phylogeny into classifications relied on the 'probable phylogeny' (Cain 1956; Michener and Sokal 1957), a practise that was neither unanimously accepted (Gilmour 1961; Gilmour and Walters 1964) nor objective. Recent years have seen an explosion in the number of algorithms and analytical tools available for reconstructing phylogenies, using both morphological and nucleotide sequence data. In particular, the rise of the discipline 'molecular phylogenetics' has revolutionised our ability to reconstruct relationships among and within different groups of organisms. Improved methods for generating rigorous hypotheses of phylogeny do not only impact on classifications; they also provide an

important framework for studying evolution, at both micro- and macroevolutionary levels. For example, comparative studies on trait evolution, diversification and historical biogeography provide a means by which to better understand the origin and evolution of biological diversity. In turn, this deeper evolutionary understanding can be incorporated into generating the most predictive classifications. Without the context of a phylogeny, patterns of character evolution would be interpreted very differently and, as a result, observed patters of variation in nature would be differently described, categorised and named.

Groups in which these recent developments have been particularly fruitful are those with a highly specialised morphology that is usually a result of adaptation to a particular life style. Convergent evolution of traits under selection and/or reduction of traits that may be informative for classification in other groups mean that these groups are difficult to place systematically on the basis of morphology alone. Plants adapted to an aquatic or parasitic life style provide typical examples. Hydatellaceae, a small family of tiny aquatic plants, was previously placed in the Monocots along with grasses and sedges on the basis of its grass-like appearance (Fig. 1a). Recent molecular phylogenetic analyses have demonstrated that it is in fact closely related to Nympheales (the water lilies), positioned near the root of angiosperms (Rudall et al. 2007; Saarela et al. 2007; Rudall and Bateman 2010). Another example is provided by *Rafflesia*, a genus of parasitic plants from the tropics of the Old World. These plants produce the largest flower known (Fig. 1b), but lack leaves, stems and roots (Nais 2001). This reduced morphology obscures their systematic position based on morphology alone. Molecular phylogenetic analyses have revealed that they are relatives of violets and poinsettias, positioned in the Malpighiales (Barkman et al. 2004; Davis and Wurdack 2004). The study of Barkman et al. (2004) also revealed that another genus of tropical parasitic plants, *Mitrastema*, traditionally placed together with *Rafflesia*, is instead a relative of heathers and blueberries in the Ericales. This finding illustrates how valuable studies of this nature are: the shared morphological characteristics of these two groups misled systematists into grouping them together, when their similarities do not reflect shared ancestry but convergent evolution upon independent adaptation to similar life styles. Another notoriously difficult group are the grasses (Poaceae). Their reduced floral morphology – a result of specialisation to wind pollination (Fig. 1c) (Linder 1998) – means that variation in many morphological traits, that have been useful for classification in other groups, is minimal (E. Anderson, in Stebbins 1956). The present thesis addresses some of the gaps in our understanding of the phylogeny, evolution and classification of grasses, with particular reference to generic delimitation in subfamily Danthonioideae.

Figure 1. Plant groups in which reduced morphologies or peculiar adaptations have rendered their systematic placement or internal classification difficult. a) Grasslike morphology of *Trithuria bibracteata* (Hydatellaceae), photo from www.flickr.com; b) Giant flower of *Rafflesia arnoldii* (Euphorbiaceae), photo from http://www.parasiticplants.siu.edu; c) Individual florets of *Cortaderia pilosa* (Poaceae), photo by M. Pirie.

Danthonioideae are a fascinating group of grasses, comprising about 280 species (Linder et al. accepted manuscript) distributed on all continents in the Southern Hemisphere, except Antarctica, with a few species native to North America and Eurasia as well. Morphologically, Danthonioideae are defined by the presence of haustorial synergids[1] in the embryo (Philipson and Connor 1984; Verboom 1994) and can further be characterised by C_3 photosynthesis, three-lobed lemmas (consisting of a central awn and two lateral lobes; Plate 5C) and ciliate ligules (Linder and Barker 2005). The subfamily is monophyletic and clearly distinguished from the Arundinioideae (the "tall, reedy grasses") within which it was previously classified (Barker et al. 1995, 1998; Barker et al. 2001). The horticulturally famous pampas grasses (*Cortaderia*; Plates 1B and 2H) belong in this group, as do the wallaby grasses (*Rytidosperma* s.l.; Plates 1–10), upon which the Australian sheep industry was based (Lodge and Groves 1990), and the snow grasses (*Chionochloa*) that dominate large areas of New Zealand's tussock communities (Plate 1J). The group is most diverse in Southern Africa, however, where there is even a vegetation type named after one of the genera (Karroid *Merxmuellera* mountain veld (Acocks 1975)). Danthonioideae are ecologically and morphologically diverse (see Plates 1–10) and geographically widespread, yet too young to be of Gondwanan origin (Christin 2008; Bouchenak-Khelladi et al. 2010), providing ample scope for addressing a range of evolutionarily interesting questions. The same factors that make this group interesting to a systematist are likely also to underlie the taxonomic "mess" that has surrounded these grasses for the past decades (Linder and Barker 2005), especially at the generic level. In fact, the generic circumscription of Danthonioideae has been unstable for over a century (Fig. 2). Not only has the generic classification of this group been controversial, but until relatively recently little was known about the diversification and biogeography of this group.

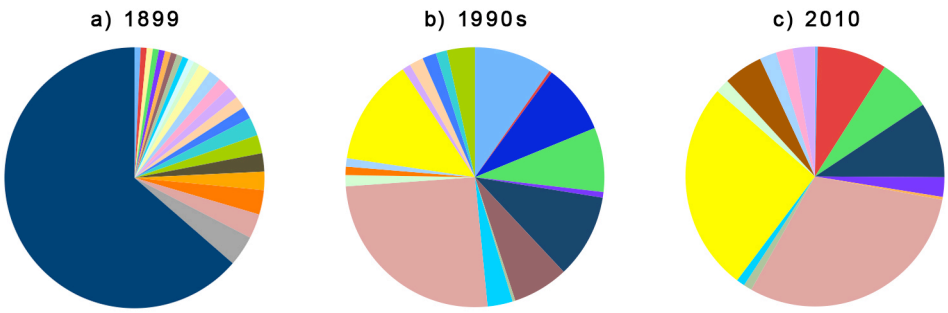

Figure 2. Changing genus concepts through time, illustrated in Danthonioideae by how the distribution of species among genera has changed over time. Dark blue = *Danthonia*; Dirty pink = *Pentaschistis/Pentameris*; Yellow = *Rytidosperma.* a) By the end of the 1890s, before Stapf's (1899) revision, the species currently in Danthonioideae were distributed among 25 genera but over half of the species were placed in *Danthonia*. b) A century later, many more genera had been described to accommodate both the variation among the species and the growing number of described species. Species were more evenly distributed among genera, the largest genus being *Pentaschistis* with 25% of the then recognised species. c) Recent redelimitation following molecular phylogenetic analysis has led to a solution that is intermediate between the two previous extremes (see Linder et al. accepted manuscript). The number of genera has been reduced from 19 to 15 with *Pentameris* and *Rytidosperma* each containing ca. 1/3 of the recognised species.

[1] An unusual embryological feature, perhaps with a role in nutrient uptake by the megagametophyte, as well as secretion of substances to guide pollen tube entry into the ovule. Synergid = either two of the haploid nuclei beside the egg cell. Haustorium = a slender outgrowth specialised for nutrient absorbtion (usually parasitic plants, plant stem or roots, or fungal hyphae).

The work presented in this thesis was performed as part of a global collaborative research effort on the systematics and evolution of the Danthonioideae[2], the results of which have already led to an improved classification for the entire subfamily and the newly discovered relationships have implications for trait evolution, herbivore defence strategies and austral biogeography. A rigorous phylogenetic hypothesis for Danthonioideae (Barker et al. 2000; Barker et al. 2007; Pirie et al. 2008) provides the basis for a string of systematic findings. *Cortaderia*, previously thought to be a genus disjunct between southern South America and New Zealand, is paraphyletic, split along continental lines (Barker et al. 2003). African genera *Tribolium, Schismus and Karroochloa* do not form monophyletic groups based on molecular data, suggesting that the similarities in spikelet morphology among the species are probably the result of convergent evolution (Verboom et al. 2006). The large African genus, *Pentaschistis*, is not monophyletic with respect to *Pentameris* and *Pseudopentameris* (Galley and Linder 2007) and exploration at the species level within this group is not complete (Galley and Linder 2006). These new systematic findings have provided a basis for novel evolutionary insight, including improved understanding of role of herbivory pressure in shaping the morphology of these species. In the African genus *Pentameris* a sophisticated defence system is achieved by interplay between leaf anatomy and leaf glands (Galley and Linder 2007) and in New Zealand absence of large herbivores is thought to have led to an increased proportion of species (primarily in *Chionochloa* and *Rytidosperma*) that are able to shed old leaves and thereby increase biomass production (Antonelli et al. submitted). At the genome level, gene tree conflict reveals a pattern compatible with an ancient hybridisation event between ancestors of the Australian monotypic *Notochloe* and *Plinthanthesis* (Pirie et al. 2008) and sheds light on biogeographical patterns in the Southern Hemisphere and the evolution of gynodioecy in *Cortaderia* (Pirie et al. 2009). Finally, detailed analyses of the snow grasses, *Chionochloa*, improve our understanding of patterns of endemism and biogeography in New Zealand (Pirie et al. 2010). Despite much important progress, a gap remains regarding our understanding of how variation is packaged among the ca. 70 species in *Rytidosperma* s.l. distributed in Australasia and South America, what their relationship to their close relatives in Africa is, and what forces might underlie some of these patterns.

In this context, the contribution of my thesis has been to determine the optimal generic delimitation for the members of *Rytidosperma* s.l. and allied African genera, based on evidence from phylogenetic analyses of both molecular and morphological data and against a background of ecological and geographical data (Chapter 2; Humphreys et al. 2010) and an investigation of the evolutionary consequences, in terms of lineage persistence and diversification, of losing a 'key trait', exemplified by danthonioid species that have lost their hygroscopically active awn (Chapter 3; Humphreys et al. submitted). In addition, and in light of incorporation of molecular phylogenetics into systematics research, the thesis also includes a detailed review of historical and contemporary generic delimitation practice (Chapter 1; Humphreys and Linder 2009).

In **Chapter 1** I investigate whether changes in concept or changes in data drive changes in prevailing genus sizes. This issue is particularly topical in an age of incorporating molecular phylogenetics into generic classification, with emerging debates about the size of genera that should be recognised (the question of rank). I review a vast amount of historical literature on genera and synthesise a summary of changes in prevailing genus sizes, development of genus concepts and shifts in data used over time. I also survey four leading journals of plant systematics for cases of generic delimitation in the past decade to gain an understanding of contemporary

[2] Collaborators on this project, led by Peter Linder at the University of Zurich, include Nigel Barker and Tony Verboom in South Africa; Marcelo Baeza in Chile; Neville Walsh, Bryan Simon and the late Surrey Jacobs in Australia, Henry Connor, Kelvin Lloyd and Bill Lee in New Zealand; and previous and current members of the Linder research group in Zurich: Chloé Galley, Mike Pirie, Rafael Wüest and Alexandre Antonelli.

prevailing genus sizes, concepts and data employed. Using these approaches I show that there is a significant bias in contemporary generic delimitation toward the recognition of more broadly construed genera, defined on the basis of molecular data under the concept of monophyly. Further, there has been a significant increase in the number of generic redelimitations carried out in the past five years, compared to the preceding five years. Summarising both historical and contemporary information I conclude that shifts in generic concepts drive changes in overall genus sizes, that the current trend toward recognising larger genera is a result of a return to study on a broad scale, rather than of incorporation of molecular data, and I predict and that classifications consisting of more broadly construed genera will be more stable and will lead to classifications in which information content and communicative power are maximised.

In **Chapter 2** I investigate whether a plastid tree, being based on a single genome, can trace enough of the species phylogeny to be useful as a basis for a reconsideration of a generic classification of wallaby grasses and allies (*Rytidosperma* s.l., Danthonioideae). This issue is particularly relevant at a time when an increasing number of generic revisions are being based on the results of molecular phylogenetic analyses, often of data from a single genome, and when there is accumulating evidence that phylogenetic hypotheses based on plastid data may be misleading, due to molecular processes that do not track evolutionary history at the organism level. A critical approach to such problems is particularly important in a group such as grasses, where interspecific hybridisation is known to occur. I present the first densely sampled and well resolved gene tree for *Rytidosperma* s.l., based on chloroplast DNA (cpDNA) and inferred by both parsimony and Bayesian methods. Resolution of relationships within this group required a tremendous input of data (~13,000 aligned base pairs) and extensive analyses. I assess the fit of the resulting cpDNA tree with morphological, ecological and distribution data as follows. A cladogram based on morphological characters was compared to the cpDNA tree by node-by-node inspection of incongruence and by use of Wilcoxon's signed rank test to assess the difference in rescaled consistency index (RC) of each morphological character across the morphological and molecular topologies. Finally, distribution of character states of the best fitting morphological characters (highest RC on each of the two topologies, respectively) were compared to their distribution across randomly generated topologies. Fit of the plastid tree with ecological and distribution data was assessed by comparing distribution of character states on the observed topology against a null of randomly generated topologies. Using these approaches I show that the plastid tree is significantly different from the morphological cladogram and show that this is the result of high levels of homoplasy in the morphological data set. Treated individually, however, several morphological characters fit the plastid tree very well. Similarly, there is a good fit between the plastid tree and ecological and distribution characters and with biogeographical patterns in the Southern Hemisphere. I conclude that a significant level of the species phylogeny is resolved by the plastid tree and I am confident it forms a sound basis for a reconsideration of generic limits. A new generic classification for the ca. 100 species concerned is informally proposed.

In **Chapter 3** I investigate the evolutionary consequences of losing traits that are known to be ecologically advantageous. To do this I use the Danthonioideae as an example because several species lack the otherwise widespread and conspicuous hygroscopically active 'bristle', or awn (Plates 4G, 9D and 10B). This structure, a conspicuous part of the diaspore (Plates 7B, 7C and 10B), is known to be important for diaspore burial and establishment, but it has never been investigated in a macroevolutionary context. I use a phylogenetic approach to infer the evolutionary consequences, in terms of lineage persistence and diversification, of losing awns. I also quantify variation in a suite of diaspore traits that are associated with the awned or awnless state and test for correlated evolution with life history. Using a range of

statistical analyses I show that awns have been lost several times and that, overall, lineages in which awn loss occurs diversify little and do not persist. Only in two small African genera have awnless ancestors diversified to form clades of primarily awnless species. Awnless diaspores are significantly smaller and rounder than awned diaspores and shifts to an annual life history are more frequent in awnless lineages than in awned lineages. Persistence of the awnless state in these clades is therefore likely to have been conferred by an ecological shift from reliance upon active burial, driven by hygroscopic activity, to reliance upon stochastic burial (i.e. a shift in 'burial syndrome') and by colonisation of habitats suitable to annuals but where not having an awn is no longer a disadvantage. I believe that these findings advance our understanding of the ecological and evolutionary contexts in which key traits may be lost and, in particular, of the biology of awns.

I hope that this thesis will have lasting impact in the field of generic delimitation, in having identified a major dichotomy in the outcomes of generic realignment depending on the type of study. I hope that, even among those who disagree with my conclusions, these findings will encourage people to carefully consider what they are classifying, why and based on what evidence. More specifically, I hope that the recognition of a more broadly construed *Rytidosperma* will prove a lasting solution to generic delimitation in a difficult group of grasses. Further, I hope my findings regarding the loss of ecologically important characters will inspire similar studies of other characters in other groups that will enable a more general understanding of how traits evolve and organisms diversify. Finally, I hope that you will enjoy reading this thesis.

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Plate 1

Plate 2

Plate 3

Plate 4

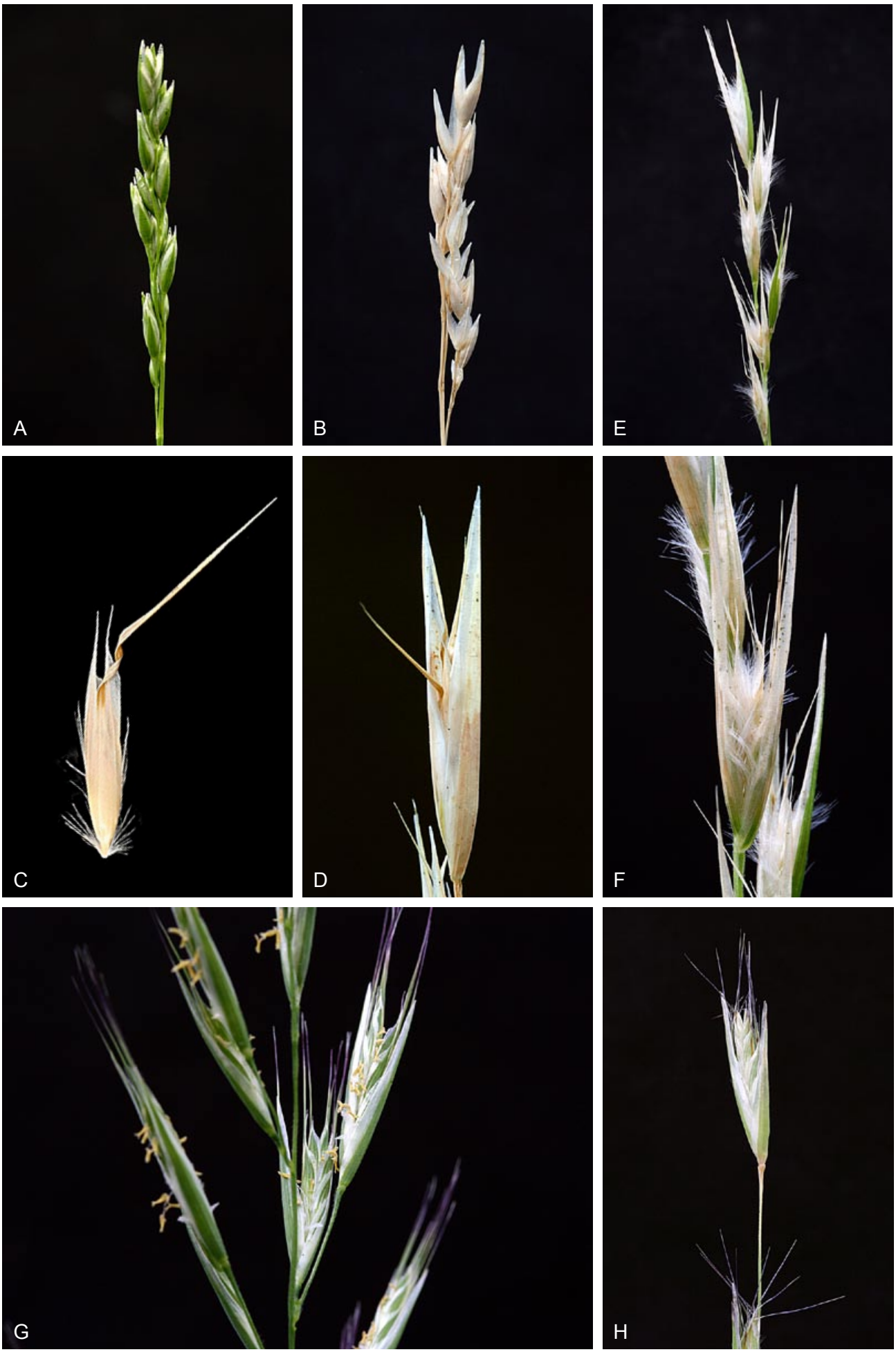

Plate 5

Plate 6

Plate 7

Plate 8

Plate 9

Plate 10

Plates 1–10. The beauty and diversity of danthonioid grasses.

Plate 1. *Rytidosperma vickeryae* in the Australian highlands (A). *Cortaderia pilosa* in the Chilean highlands (B). *Rytidosperma pilosum* in the Australian lowlands, at anthesis (C). *Rytidosperma semiannularis* – dispersal in action! (D). Hairy sheaths of *Rytidosperma pilosum* (E). *Notochloe mircodon* gutting out over river in the Australian Blue Mountains (F). *Rytidosperma nudiflorum* in the Australian highlands, sod tussock grassland (G). *Pentameris pallida,* here pictured as a weed in South Australia (H). Creeping rhizomes of *Rytidosperma lepidopodum* (I). *Chionochloa* sp., tall tussock grassland in New Zealand (J).

Plate 2. *Rytidosperma* spp. in eucalypt forest understory (A). *Rytidosperma geniculatum* in lowland Australia (B). Red, dangly anthers of *Rytidosperma pallidum* in lowland Australia (C). *Rytidosperma pictum* with impressive roots, high in the Andes (D). *Rytidosperma australe* in the New Zealand South Island highlands (E). *Rytidosperma telmaticum*, in a kettle hole the New Zealand South Island inland basin (F). *Chionochloa frigida* in the Australian highlands (G). *Cortaderia* sp. in Chile (H).

Plate 3. *Rytidosperma buchananii.* Part of inflorescence, at anthesis (A). Inflorescence turning infructescence (B). *Rytidosperma longifolium.* Part of inflorescence, at anthesis (C). Single spikelet, at anthesis (D). *Rytidosperma unarede.* Part of inflorescence, with individual spikelets at anthesis visible (E). *Danthonia spicata.* Spikelet with several florets inside (F).

Plate 4. *Rytidosperma pulchrum.* Part of inflorescence with individual spikelets at anthesis visible (A). Spikelets with florets inside, at anthesis (B). Spikelets, either as empty glumes (top) or with mature fruit (caryopses) inside (left) (C).

Plate 5. *Danthonia decumbens.* Inflorescence (A). Infructescence (B). *Danthonia intermedia.* Single floret, showing the tri-lobed lemma with a twisted awn in the centre and the hairy callus below (C). Single spikelet with an awn popping out between the glumes (D). *Danthonia malacantha.* Inflorescence (E). Part of inflorescence, focussing on a single spikelet (F). *Rytidosperma quirihuense.* Part of inflorescence, at anthesis (G). Single young spikelet, with individual florets visible between the glumes (H).

Plate 6. *Rytidosperma gracile.* Part of infructescence with mature (or maturing) caryopses inside (A). Part of inflorescence, at anthesis (B). *Rytidosperma maculatum.* Single spikelet at anthesis with awns emerging at the top (C). Inflorescence (D). *Danthonia araucana.* Spikelets at anthesis (E). *Danthonia californica.* Single spikelet with its seven individual florets, embraced by the glumes (F). *Rytidosperma clavata.* Part of infructescence (G). Note the tightly twisted awn column (dark brown) of the very long awns.

Plate 7. *Rytidosperma carphoides.* Inflorescence (A). Part of maturing inflorescence, with the caryopses (beige) visible though the lemmas of the two top florets (=diaspore) (B). Infructescence (C). Single diaspore at top of infructescence, showing white lemma hairs (D).

Plate 8. *Rytidosperma semiannulare*. Inflorescence at anthesis (A). Part of inflorescence at anthesis (B). Single spikelet at anthesis (C). *Rytidosperma nudiflorum.* Part of inflorescence at anthesis (D). *Rytidosperma paschale.* Single spikelet with florets visible between the glumes (E).

Plate 9. *Rytidosperma setaceum* (morphotype 'big'). Part of inflorescence (A). Single spikelet at anthesis (B). Single spikelet at anthesis (C). Infructescence with tightly corkscrewed awn columns (brown) clearly visible (D). *Rytidosperma pilosum* (morphotype 'dark'). Part of inflorescence at anthesis (E). Single floret at anthesis (F). Note younger stamens still inside florets and older stamens dangling their anthers, ready to catch the wind.

Plate 10. *Rytidosperma pilosum* (morphotype 'dark'). Spikelets at anthesis (A). Mature spikelets with diaspores inside, containing carypses and displaying tightly twisted awn columns (B). *Rytidosperma richardsonii*. Inflorescence turning infructescence (C). Part of young inflorescence (D). Detail of inflorescence, showing individual florets inside spikelets, with white lemma hairs clearly visible (E).

Credit is due to M. Pirie for photos 1B, 2D, 2G and 2H.

Chapter 1.

CONCEPT VERSUS DATA IN DELIMITATION OF PLANT GENERA

A.M. Humphreys and H.P. Linder

Taxon 58, 1054-1074. 2009.

"…the concept of the genus / …/ may vary not only with the individual's interpretation, but it may vary more or less in accordance with the trend of the times. This is perfectly natural, since we are all influenced to a greater or lesser degree by the opinions of our contemporaries."

Greenman (1940, pp. 371-372)

Abstract

As a consequence of there being several ways in which observed patterns of variation in nature can be conveyed in a generic classification, long recognised genera have changed in size over time. The generic rank has its origins in folk taxonomy, where genera were homogenous units of relatively few kinds. In the era of Bentham there was a widespread preference for large genera, many of which were split during the 20th century. In a survey of contemporary (1998–2007) generic delimitation practice we found a significant dichotomy between studies that incorporate molecular data and those that rely exclusively on morphological data. The former lead to delimitation of larger genera whereas the latter in general do not. This finding spurred a broader investigation into what drives changes in overall generic sizes, new data sources or new concepts? Two new data types have been introduced during the course of history: detailed morphology (anatomy, cytology) and chemical data (amino acid and DNA sequence data). Conceptual development has seen several turns: from language and communication, through memory and stability, to evolution and monophyly. We argue that conceptual change has a greater impact than changes in data do, since new data must be interpreted and translated into a classification and since conceptual changes may spur a search for new kinds of data. We conclude that the current trend toward recognising larger genera is a result of a return to study on a broad scale, rather than of incorporation of molecular data.

Introduction

'What genus is it?' is often the first question to spring to a biologist's mind when carrying out identification or biodiversity-related work (Oberwinkler, 1994). Considering that the genus is part of the way in which we communicate the natural world, and that it is often in widespread use beyond the scientific community, the generic rank is arguably the most important 'to get right' (Oberwinkler, 1994; Backlund & Bremer, 1998).

Genera are groups of species, in rare cases single species, that in some respects may 'exist' in nature and in others exist simply by means of definition (e.g., Anderson, 1940; Greenman, 1940; Stebbins, 1956; Walters 1963, 1986). Genera have a rank, meaning that they have a defined place in a hierarchical system (Hennig, 1966; Funk & Stuessy, 1978; Pfeil & Crisp, 2005), and are part of how we refer to species, *Genus species*, which is simply a noun-adjective combination. Grouping of species into genera allows representation of recognised patterns (Jeffrey, 1987) in such a way that genera serve as memory devices (Raven & al., 1971; Clayton, 1974, 1983; Stevens, 1997) and as units for information storage and retrieval (Cronk, 1990; Barkley & al., 2004). For example, someone looking for information on *Fagus* L. or *Quercus* L. knows by the way in which they are written that they are genera and knows that they are mutually exclusive (Barkley & al., 2004).

'Good' genera are predictive and stable. 'Predictiveness' allows prediction of attributes of taxa that may not yet be characterised or described (Clayton, 1983; Stace, 2005; Pfeil & Crisp, 2005). 'Stability' increases communication power of a classification by perpetuated use of already accepted names (Stevens, 1985) and is maintained by delimitation of genera in such a way that future nomenclatural changes will be unnecessary. Both predictiveness and stability are most likely realised if the species that form a genus have a 'real' connection among them. This may most appropriately be a historical one (Kornet, 1994), through descent with modification, and thus 'good' genera are monophyletic (Funk, 1985; Oberwinkler, 1994). We agree with Walters (1963, 1986) and Cronk (1990) that efforts to define a genus that reflects evolutionary patterns (expressed by monophyly) should not override those that ensure its usefulness. Consequently, monophyly is important only in so far as it increases the chances of a genus being both stable and predictive. Further, a classification that does not convey evolutionary units may be misleading since it is likely to be interpreted as doing so. Otherwise, usefulness of a genus may be more directly related to size: genera that are not too big or too small (Clayton, 1972; Oberwinkler, 1994) are easier to handle and memorise (Clayton, 1974, 1983; Stevens, 1997; Frodin, 2004). Additionally, diagnostic characters may best convey utility and memorability (Stevens, 1985). In short, good genera are stable and predictive and useful genera are diagnosable and of a workable size. Monophyly will most likely ensure both stability and predictiveness and in turn lead to unambiguity and broad acceptance, reinforcing stability (Albach, 2008).

Despite a reasonable amount of agreement among systematists regarding the attributes of good genera, generic sizes have fluctuated over time and throughout its history the practice of generic delimitation has seen several trends (Greenman, 1940). Here we discuss generic delimitation practice in a historical and contemporary realm to investigate what drives changes in prevailing genus size—changes in concept or access to new types of data (summarised in Fig. 1)? While our focus has been the generic rank, parts of the discussion below could be extended to the family rank as well. Species, on the other hand, would require a separate analysis.

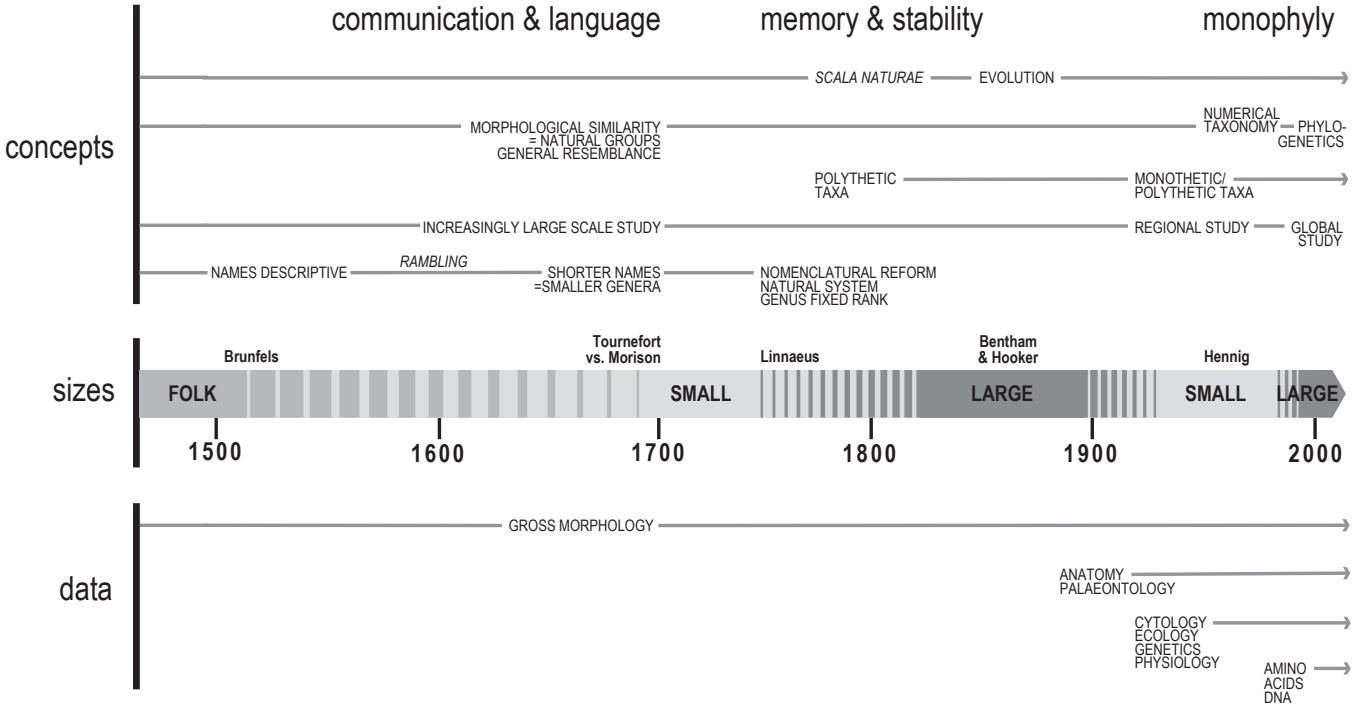

Figure 1. Timeline showing development of generic sizes, concepts and data used in generic delimitation. Sizes. Already by the time of Linnaeus there were differing opinions regarding the ideal inclusiveness of genera. Folk genera are generally broad, Morison (following Cesalpino) elaborated on folk use, Tournefort recognised many, small genera and Linnaeus sunk many of Tournefort's genera. In the grand works of Bentham and Hooker and other prominent nineteenth century botanists synthesis prevailed and variation among species was expressed as subgenera. During the twentieth century many of the larger genera of the previous century were split, but in recent years there seems to be a growing trend toward their renewed recognition at the generic rank. **Data.** There have been two major shifts in data: detailed morphology (e.g., anatomy, cytology, ecology) and chemical data (largely DNA sequences). **Concepts.** Genera originated from the need to describe and communicate patterns observed in nature. During the seventeenth and eighteenth centuries morphological similarity in all sorts of characters was taken to signify natural groups. Descriptive names meant that the size of a genus dictated the length of its name. Linnaeus fixed the rank of the genus and laid down strict rules how genera were to be named. Toward the end of the eighteenth century polythetic taxa came to be recognised in botany. A belief in the *scala naturae* meant that delimitation of groups was dictated by their size. In the nineteenth century the idea of a *scala naturae* was replaced by the theory of evolution and size differences among genera came to be accepted. Genera were delimited so that classifications should remain stable and so that all the genera could be memorised. Eventually, this system was replaced by one in which monothetic taxa defined on a local basis were recognised. Finally, monophyletic genera representing evolutionary lineages, studied on a global basis, are coming to characterise the early twenty-first century.

The size of the genus through time

Linnaeus and his antecedents

Perhaps one of the earliest published works that can be used to trace the historical development of changing genus sizes is Brunfels' herbal (*Contrafayt Kreuterbuch*, 1532–1537). In this, genera represent the smallest grouping requiring a name and consist of only one or a few 'kinds', given uninominal names in Latin (Bartlett, 1940). Additional names distinguish several kinds, but if only one kind is present, the genus name alone is sufficient to describe it.

Brunfels' work was very simple, but during the 100 years or so that followed, this simplicity was lost and was not restored until Tournefort's (1694, 1700) use of single, or in rare cases two, words to denote genera. Since generic names were descriptive at that time, Tournefort achieved his brief names by splitting larger genera. He recognised exactly 698 genera (Raven & al., 1971) and criticised his contemporary, Morison, for recognising only 200–300, larger genera, with internal variation expressed as 'minor genera' (Bartlett, 1940; Raven & al., 1971; Atran, 1990). In order to express what was common to all the kinds, Morison (1672) combined generic, 'minor generic' and specific designators in names that were so long that they could "hardly be uttered with one breath, and [went] two or three times across the printed page" (Bartlett, 1940: 361).

Linnaeus thought that there were as many genera as there are "differently constructed fruit bodies among species" (Linnaeus, 1751: 159) and reduced many of Tournefort's genera that were based on other types of characters (Stafleu, 1971; Atran, 1990; Farjon, 2005). He believed in grouping by tens and established a baseline classification that could accommodate 10 classes, 100 orders (families), 1,000 genera and 10,000 species and that allowed the classification of all plant species known to him (5,900 species were included in *Species Plantarum*; Linnaeus, 1753) (Cain, 1958; Stevens, 2002). Both narrow and broad generic concepts can be found in his work (Stafleu, 1971); "very many" of his genera consisted of only a single species and others consisted of a "large number of them" (Linnaeus, 1751: 203). He warned against deceptive similarity among genera and said that "one must not reduce the natural orders to genera, nor indeed, eventually the classes too. Large genera would lead to total confusion" (Linnaeus, 1751: 205). Importantly, Linnaeus did not make use of intermediate ranks and used the genus to denote the smallest group above the species (Cain, 1958). A preference for smaller genera remained among followers of Tournefort and Miller into the early 19th century through the work of Cassini, Gasparrini, Rafinesque, Klotzsch and Miquel (Frodin, 2004).

Bentham's large genera

Increasingly, as access to good herbaria and good libraries became more widespread, voices for the recognition of large genera were expressed. At this time, a number of major botanical works were published, including those of the de Candolles (e.g., 1824–1873, 1874–1896), Kunth (1833–1850), Endlicher (1836–1850), Bentham & Hooker (1862–1883) and Engler & Prantl (1887–1915) (Frodin, 2004). Synthesis prevailed in these works, carried out on the scale of the entire plant kingdom. Bentham, in his collaborative work with Hooker (1862–1883), was explicit about his liking for large genera, with variation accounted for by the interpolation of a complex hierarchy between formal taxonomic ranks (Stevens, 1997, 2002). As more and more new plants were discovered increase in size took place sooner in genera with a predominantly temperate distribution (e.g., *Carex* L., *Euphorbia* L., *Quercus* and *Salvia* L. or more locally *Erica* L. [Southern Africa], *Eucalyptus* L'Hér. and *Acacia* L. [Australia]) or with a lowland tropical distribution (e.g., *Cassia* L. *s.l.*, *Croton* L. and *Ficus* L.) (Frodin, 2004). The largest genera in existence in 1883 (published by N.E. Brown, 1883 using figures from Bentham and Hooker's *Genera Plantarum*) were *Solanum* L., *Piper* L., *Ficus, Eugenia* L., *Psychotria* L. and *Croton*, in tropical and subtropical areas, *Senecio* L. and *Euphorbia*, with

almost global distributions and *Astragalus* L. and *Carex*, in (north) temperate regions. Their sizes ranged from 500–900 species (Frodin, 2004).

Segregation of satellite genera

Toward the end of the 19th and early 20th century, many of Bentham's genera had grown so large that their size was becoming an impediment to their study (Frodin, 2004). Nevertheless, size alone was not justification enough for them to be split (Stevens, 1997) and the emerging pattern was a single large genus ('core' genus; Funk, 1985) accompanied by several, often quite small, 'satellite' genera (Cronk, 1990; Frodin, 2004). Bentham included several of the segregate genera that were described before or during his time, into a number of older genera, such as *Panicum* L., *Crepis* L. and *Andropogon* L., that came to contain many synonyms. During the intensive splitting that took place throughout the 20th century these were revived and reinstated at the generic rank (Greenman, 1940). For example, *Astranthium* Nutt., a monotypic genus proposed by Nuttall (1841) was reduced to synonymy under *Bellis* L., but was resurrected by Larsen (1933). *Youngia* Cass. of Cassini (1831) was regarded for many years as synonymous with *Crepis*, but was reinstated as a valid genus by Babcock & Stebbins (1937).

Early twenty-first century

Lately, it seems many 'core' genera have been enlarged by reduction to synonymy of associated satellite genera (Frodin, 2004). *Euphorbia* (Euphorbiaceae) has been expanded to include *Endadenium* L.C. Leach, *Monadenium* Pax, *Synadenium* Bioss. and other satellites, making it widespread genus of 2,160 species, equivalent to Euphorbiinae (Bruyns & al., 2006); *Dryandra* Thunb. (93 spp.) has been transferred to *Banksia* L. f. (80 spp.) (Proteaceae), creating a single genus, equivalent to the subtribe Bankiinae (Mast & Thiele, 2007); *Hibiscus* L. (Malvaceae) (~350 spp.) has been expanded to include a number of embedded genera (Pfeil & Crisp, 2005); *Corymbia* K.D. Hill & L.A.S. Johnson (113 spp.) and *Angophora* Cav. (9 spp.) have been subsumed by *Eucalyptus* (~600 spp.) (Myrtaceae) (Brooker, 2000; but for arguments and evidence against this see Ladiges & Udovicic, 2000; Parra-O. & al., 2006); *Symbegonia* Warb. has been reduced to a synonym of *Begonia* L. (Begoniaceae), creating a genus of over 1,400 species (Forrest & Hollingsworth, 2003); several Southern Hemisphere Plantaginaceae genera (*Chionohebe* B.G. Briggs & Ehrend., *Derwentia* Raf., *Detzneria* Schltr. ex Diels, *Hebe* Comm. ex. Juss. [~90 spp.], *Hebejeebie* Heads, *Heliohebe* Garn.-Jones, *Leonohebe* Heads and *Parahebe* W.R.B. Oliv.) have been sunk into the previously northern *Veronica* L. (~500 spp.) (Garnock-Jones & al., 2007) and the limits of *Alchemilla* L. (250–1,000 spp.) have been expanded to include *Lachemilla* Rydb. (80 spp.) and *Aphanes* L. (20 spp.) (Gehrke & al., 2008).

Similarly, a long list of monotypic segregates have been subsumed under their larger affiliate genera: *Madangia* P.I. Forst., Liddle & I.M. Liddle, *Absolmsia* Kuntze and *Micholitzia* N.E. Br. have been sunk into *Hoya* R. Br. (Apocynaceae) (Wanntorp & al., 2006; Wanntorp & Forster, 2007); *Normania* Lowe and *Triguera* Cav. (two spp.) have been subsumed under *Solanum* (Solanaceae) (Bohs & Olmstead, 2001) and *Seriphidium* (Berrer ex Less.) Fourr. and *Oligosporus* Cass. have been synonymised with *Artemisia* L. (Asteraceae) (Torrell & al., 1999).

This trend is obviously not all-encompassing and some large genera have recently been split. The formerly 1,650 species in *Psychotria* have been split into three genera: *Psychotrophum* P. Brown, *Notopleura* (Benth. & Hook. f.) Bremek. and leaving ca. 1,200 species in *Psychotria* s.str. (Nepokroeff & al., 1999). *Acacia*, previously comprising over 1,350 species, has been split into five genera (Maslin & al., 2003) and *Senecio* (1,250 spp.) has been redelimited so that eight species assemblages and *Jacobea* Thunb. are removed from *Senecio s.str.*, into which six smaller genera have been sunk, leaving ca. 1,000 species in *Senecio s.str.* (Pelser & al., 2007).

Conceptual shifts

Origin of the genus concept

Systems for naming plants can be found in almost any culture from ancient Greece, China and Mexico, through the Pacific and Asia to Africa and Europe (Bartlett, 1940; Berlin & al., 1973; Atran, 1990; Frodin, 2004). Whatever the people or the language, these systems almost invariably contain "a more or less well defined idea of the genus, as the smallest group that almost everyone might be expected to have a name for in [their] vocabulary" (Bartlett, 1940: 351; Cain, 1956, 1958; Berlin & al., 1973). Studying these names can provide insights into the mechanisms involved in the origin of the genus concept. Bartlett (1940) provides an excellent example from the island of Sumatra. People there utilise the local climbing rattan palms (Arecaceae) in various ways. These rattans are collectively referred to as *hotang* and are individually distinguished as *hotang soga, hotang djorlang* and so on. Another climbing plant, which is not a palm but a species of *Flagellaria* L. (Flagellariaceae), superficially similar to rattans, is called *hotang da ursa*. While any of the rattans can be referred to just as *hotang*, the *Flagellaria* species can not; it has to be referred to as *hotang da ursa* in full. This indicates how generic names may have arisen in different languages and also indicates that the generic concept has been "so logically and extensively applied in various parts of the world, that to trace its history would be to trace the history of language and thought itself" (Bartlett, 1940: 354; Berlin, 1992).

Generic names in folk classifications usually correspond to what in linguistics is known as primary lexemes (a word or a vocabulary item) (Berlin & al., 1973). A primary lexeme is psychologically more basic (e.g., red, yellow, oak, pine) than a secondary lexeme (pale red, yellowish, post oak, ponderosa pine), suggesting the existence of a category superordinate to the one in question and implying that the generic rank is psychologically the most salient in folk taxonomies (Berlin & al., 1973; Li, 1974). On one level then, grouping plants into genera has arisen as a matter of convenience and linguistic preference and has been established through interplay of every day use in communication and logic (Walters, 1986). On another, the concept of the genus has arisen from an essential feature we have as living beings: we have an unconscious processing mechanism in which we distinguish like from the unalike and separate the constant from the variable (Jeffrey, 1987), 'intuitive induction' of Atran (1990). Thus, the genus allows us to communicate how we see the natural world, in such a way that describing patterns and grouping into genera would seem linguistically and psychologically inevitable (Bartlett, 1940; Gilmour & Walters, 1964; Raven & al., 1971; Berlin, & al., 1973). This process is likely to have operated in two modes (Bartlett, 1940) just as it does today. First, with increasing experience, people make finer distinctions, which require nomenclatural differentiation from the original entity. The original name becomes what we recognise as the genus; variously qualified, it becomes the basis for specific names. Thus, genera originate through analysis: by separation of the species within a genus. Second, as language becomes cumbersomely rich in separate names for things that are difficult to tell apart, there is a tendency towards defining new groups based on newly perceived similarities. Thus, genera also originate through synthesis: by grouping of their constituent species.

Transition from folk botany to scientific taxonomy

The clear and simple genera present in Brunfels' herbal (1532–1537) suggest that he had a 'modern' idea of a genus, as a morphologically homogenous unit that is differentiated into one or several species (Bartlett, 1940). Brunfels was active at a time when botanical classifications were developing from their origins in folk botany and being expressed in herbals, variously organised alphabetically or by utility (Arber, 1938). At that time there was no consensus how to best divide plants into groups; new plants were simply squeezed into old genera based on affinity in all sorts of characters (Bartlett, 1940; Sloan, 1972). Descriptive generic names became polynomial and did not necessarily incorporate a generic component at all. By the time *Pinax Theatri Botanici*, an index to all known plants (Bauhin, 1623), was

published, botanical classification had become wholly divorced from language—a name had lost any indication of rank and knowing where species belong in a classification had become a feat of memory (Bartlett, 1940; Cain 1994). There followed a century of confusion, featuring most prominently Ray, Rivinius, Morison and eventually Tournefort (Sloan, 1972; Atran 1990). Their work, although vastly different, was really only elaborations of the foundations laid down by Cesalpino (1583), who had used the intuitive structure of popular taxonomy to generate easy-to-follow keys that were to aid placing exotic plants with their natural genus (Atran, 1990). But Cesalpino did not use "genus" in the fixed sense we do today and botanical classifications of the 16th and 17th centuries were constructed upon "genera" of several orders (Sloan 1972; Atran 1990).

Enter Tournefort. He restored the generic concept to simplicity and utility and is heralded by some as the originator of genera (Bartlett, 1940; Raven & al., 1971; Sloan, 1972; Atran 1990). Arber (1938) and Stafleu (1971) consider this honour belonging to Gesner, in being the first to apply to the "genus" only substantive names, only his work was less well known. Tournefort (1694, 1700) stabilised the concept of the genus and produced a simple, concise and easily memorised classification (Raven & al., 1971; Sloan 1972). He was consistent in the characters he used to delimit groups and he showed that similarity in two or three parts (roots, stems, leaves, flowers, fruits or seeds) would generally be necessary for species belonging to the same genus (Bartlett, 1940; Sloan, 1972). Tournefort erected separate genera to accommodate variation, to avoid forcing 'kinds' where they did not fit. He regarded monotypic genera as reflecting incomplete exploration and that further, allied species would sooner or later be found (Bartlett, 1940; Atran, 1990).

Tournefort's working concept, then, was morphological correspondence, close enough that simplicity could be achieved by keeping genera small, their descriptive names short, removing the need for the intermediate ranks of Morison. In contrast, simplicity to Morison meant fewer genera, but then communication of their species was complicated by their long names. In a reaction to this approach, Tournefort (1694: 38 in Atran 1990: 166) asked: "What is the necessity, for example, of following Morison in calling hops, *Convolvulus heteroclitus perenni, Floribus foliaceis, strobili instar*? Wouldn't it be better to make of it a particular genus, and to leave to it the name, *Lupulus vulgaris*, which is known the world over?" Evidently, already by the early 18th century there had been a shift from communication and simplicity being central to the concept of the genus, to chaos when too much is expressed by a name and back to clarity and utility when all known plants are placed in well-defined genera with concise names. In other words the contradiction between having many, simple genera versus few, complex genera had been established; but at that time large genera had the undesired consequence of polynomial names.

Linnaeus' nomenclatural reform, system and memory

This is the scene into which Linnaeus entered. He was, of course, not working in isolation, but largely adopted the generic concepts and names laid down by the work of his predecessors (Linnaeus, 1737, 1751; Bartlett, 1940; Walters, 1962; Stafleau, 1971; Sloan 1972; Atran 1990). Thus, Linnaeus' reform was nomenclatural rather than conceptual. It removed the dependency of the length of a name on the size of the genus and solidified the transition in generic names from being descriptive to being labels. His strict rules about how generic and specific names were to be created, firmly established the simplicity and intelligibility of common speech in Latin nomenclature (Bartlett, 1940; Atran, 1990).

Twentieth century systematists (e.g., Cain, 1958; Mayr, 1968, 1982; Sloan, 1972) have labelled Linnaeus essentialist, claiming that he deliberately classified according to the rules of logic. However, this "essentialism story" (Winsor, 2006b) is a much simplified tale of what philosophical undertone classification biology may contain and it is being pounded with blows from several corners (history: Stearn, 1959; Atran, 1990; Müller-Wille, 1999; Winsor, 2001, 2003, 2006a, b; McOuat, 2003; philosophy: Pellegrin, 1982, 1986; Wilkins, 2004, in prep; Wilson & al., in press). Avoiding any metaphysical aspect that may have been present in the work of Linnaeus and his antecedents, what remains of Linnaeus' genus concept from a

systematist's perspective? Linnaeus' second achievement was his arrangement of plants into a system. The notion of a 'system', had been introduced into botanical classification by Tournefort and Rivinius in a movement away from 'synopsis', which had prevailed in the work of Cesalpino and others in the 16th and 17th centuries (Cain, 1958; Stevens, 2002). 'Synopsis' literally comes from to 'see all together' and according to Linnaeus was appropriate for a "*key to the classes*" (Linnaeus, 1751: 154) but it should not be used at the generic level. Rather, a 'system' should be adopted, for "[t]he difference between a synopsis and a system is this: for the synopsis: *a* 2; b 4; c 8; d 16; e 32. for the system: a 10; b 100; c 1,000; d 10,000; e 100,000. Therefore a system is superior to a synopsis" (Linnaeus, 1751: 155). Thus Linnaeus placed his 'groups of ten' in a hierarchy with five levels in which "genus" denoted a fixed rank, the central rank. With that, generic uninomials came to be central in scientific taxonomy in the same way as primary lexemes had been central to folk taxonomies (Berlin & al., 1973). The basic simple folk concepts that had been lost during the Renaissance had been restored into taxonomic practice (Raven & al., 1971; Atran, 1990).

A third element of Linnaeus' work is his clarity regarding the taxonomic usefulness of different kinds of characters (Winsor, 2006a). Natural genera must be based on the "natural character" (Linnaeus, 1751: 189), which expresses all possible generic features, combining "essential" characters (those that "provide the genus to which it is supplied with its most proper and peculiar feature"; Linnaeus, 1751: 187) and "factitious" characters (those that "cannot sufficiently distinguish the genera in a natural order"; Linnaeus, 1751: 188).

Clearly, Linnaeus was analytical and he was pragmatic (Linnaeus 1751: 151, 152; Müller-Wille, 1999), aiming to produce a classification useful for diagnosis (Linnaeus, 1751: 288), in which all genera could be memorised (Linnaeus, 1737: 213, 251; 1751: 256; Cain, 1958; Stevens, 2002) and in which all plants were clearly named. If generic names were clear and related to things that could easily be identified and placed in a systematic context then they would, by virtue of that same system, be memorised (Linnaeus, 1764; Stearn, 1959; Stafleu, 1971). Pragmatic was also how he was perceived by botanists of his time. Banks wrote in a letter to Linnaeus' son in 1778: "I have invariably followed the Rules of [Linnaeus'] System /…/ so that the Plants in my intended Publication will be arrangd according to his Strictest rules. Such as are of Genera descrbd by him will have his names. The new ones, /…/ will be named Either in honor of distinguished Botanists, or, according to the Rules in Philosophia Botanica" (Chambers, 2000: 51, abbreviated spelling in original).

More fundamentally, Linnaeus believed that genera and species were the work of nature, created through processes laid down by the laws of the creator, the laws of nature, realised through the laws of man, who observes what has taken place (Linnaeus, 1764; Stearn, 1959). His main idea was that fundamentally distinct types ("*Ordinaes naturales*"), created supernaturally at the 'beginning', hybridised with each other, in a process driven by divinity, nature and chance, successively until classes, genera, species and varieties were produced (Linnaeus, 1764; Bartlett, 1940; Bremekamp, 1953; Stearn, 1959; Larson, 1971; Stevens & Cullens, 1990; Stevens, 2002). He also believed that the continuum of nature, the idea of a *scala naturae*, prominent among 18th century naturalists (Stevens, 1994, 1997), was expressed in plants at the ordinal level in the form of a constant medulla (Stevens & Cullens, 1990). His ideas on hybridisation and continuity were brought together in his belief that every hybrid that was produced expressed the medulla and fruit characters of the mother (Stevens & Cullens, 1990 and references therein). A shared medulla meant that they belonged to the same genus. New species were created when originally undifferentiated medulla was gradually modified by variation in the cortex.

Unity and stability in the era of Bentham and Hooker

A belief in the *scala naturae* meant that 18th century naturalists, Linnaeus, Adanson, Lamarck and Jussieu among others, viewed all classifications as artificial (Cain, 1958; Stevens, 1984, 1994, 1997). The only way to classify was therefore to delimit groups of a certain size (Stevens, 1994, 1997). With time, these ideas began to crumble and Cuvier, de Candolle and eventually Bentham suggested that size differences among genera may be true rather than

mere artefacts of differing opinion (Stevens, 1994, 1997, 2002; Frodin, 2004). In the sense that these size differences may have been shaped by nature, this view was confirmed by the timely publication of *On the Origin of Species by Means of Natural Selection* (Darwin, 1859). Bentham was not an immediate convert to Darwin's theory of evolution, whereas Hooker was one of the earliest and strongest supporters of it (Stevens, 1984, 1997; McOuat, 2003; Knapp, 2008). Regardless, their delimitation of taxa was driven mainly by their concerns for large genera and stable classifications. Bentham claimed that his preference for larger genera originated not from the requirements laid down by science, but from those enforced by language (Stevens, 1997, 2002). He said that it was of little importance for science what rank was given what name, "but for language, the great implement, without which science cannot work, it is of the greatest importance that the groups that give their substantive name to every species they include should remain large" (Bentham, 1858: 32). To Hooker, this apparent conflict between science and language was related to the difficulty of changing a classification that is already in use: "to express [systematists'] views scientifically we must break up the whole nomenclature, & rather than do this excessively, we confine ourselves to stating our views without acting on them" (original citation of Hooker's correspondence with Darwin in Burkhardt & Smith, 1991: 25). These quotes suggest that a classification is the most useful if it can be memorised and if it remains stable. To achieve this, Bentham and Hooker attempted to keep the number of genera low, avoid monotypic genera—they might clutter the memory (Stevens, 1997, 2002; Frodin, 2004)—and retain old genera and ignore new genera to avoid the inconvenience of change (Stevens, 1997).

Differing beliefs in evolution had little tangible effect on their classification practice. Nevertheless, Bentham (1864) was clear about how differing concepts could affect classification. He noted that the smaller genera included in de Candolle's (1824–1873) work were probably the result of the large numbers of contributors involved (himself included), causing loss of unity (Stevens, 1997). Study on a broad scale, both geographic and taxonomic, must have played an influential role on generic concepts at that time, but since this requires either a lot of time or effort, preferably both, it is easy to see how the increase in size of large genera soon became an impediment to their continued study.

New Systematics and the flora era

In the 1930s Fisher (1930) laid the foundations of what is now known as population genetics, by providing a connection between Mendelian genetics (Mendel, 1866) and Darwinian natural selection (Darwin, 1859). These theories were later unified into a single, sound account of evolution; the 'Modern Synthesis' (Huxley, 1942). In taxonomy these developments led to the pursuit to discover the products of evolution and the evolutionary forces that act upon them in nature. Taxonomists began to draw on knowledge and research methods from other fields of biology in what is known as experimental taxonomy or New Systematics (Huxley, 1940). Descriptive taxonomy and experimental genetics were combined by Anderson, Babcock and Turrill to better understand 'critical' genera, such as *Iris* L. and *Crepis* (Hagen, 1984; Vernon, 1993). However, Mayr urged taxonomists to redirect their attention to the species (Winsor, 2006b) and Anderson (1940) was explicit about the confines of genetics and cytology to studying evolution at the specific rank, since very few intergeneric crosses were found to yield fertile hybrids. Genera had been reduced to 'units of convenience' that were discussed "in passing" by Huxley (1940: 3) or in terms of the evolutionary processes that underlie the formation of species versus those that underlie the formation of genera (Anderson, 1937, 1940; Stebbins, 1956), but not in terms of their central role in upholding a useful classification.

In a 'survey of modern opinion' Anderson (1940) captured the status of genera relative to the status of species in the minds of 50 contemporary taxonomists. He found differing opinions depending on age and taxonomic experience. Monographers tended to believe that genera are the more natural unit and that the same evolutionary processes are involved in the formation of both genera and species and as a consequence morphological differences between genera might be of the same kind as those between species. Non-monographers

(taxonomists with experience in other biological disciplines) believed the opposite or were in partial agreement with the view above. Older "men" (*sic*) showed little interest in the survey and said that it was inappropriate to discuss genera in this way, whereas younger men (under 40) responded with enthusiasm. These findings reflect the notion that the genus is the smallest 'kind' of plant or animal that can be recognised without close study (Cain, 1956; Berlin & al., 1973) but that 'close study', e.g., by experimental taxonomists, leads to the notion that species can be defined as distinct units with an objective existence in nature, different to that of other ranks (Huxley, 1940). This survey also demonstrates how genus concepts change with the trends of the times and, importantly, reveals the presence of a growing dichotomy between those who studied the products of evolution (monographers) and those who were also concerned with the processes thereof (non-monographers).

Research developments of the New Systematics were disastrous for taxonomy. Detailed investigation, often of only a limited portion of larger genera, along with a distinct dislike for large genera (Clayton, 1972), led to (artificial) splitting (Robinson, 1906) that made sense only on a local scale (Stevens, 1997, 2002; Paton, 1999; Frodin, 2004). Newly found variation was increasingly expressed at the generic rank, in a revival act of Tournefort's practice of generic delimitation. It was quite literally so, for many of Tournefort's smaller genera were recognised at the generic rank during the mid 20th century (Davis & Heywood, 1963). Bentham (1864) had previously warned that studies of restricted geographic and taxonomic scope might lead to excessive subdivision of groups with little thought of the consequences (Stevens, 2002). In America, Robinson (1906) had similarly condemned a splitting movement led by controversial botanists Britton and Greene (Dupree, 1959; Kingsland, 2005), for causing loss of information about groups that once were an entity. In the mid 20th century similar concerns were raised (Arkell & Moy-Thomas, 1940; Bartlett, 1940; Sprague, 1940; Corner, 1961; Walters, 1962; Clayton, 1974).

Curiously, the literature seems to lack explicit justifications, from a theoretical or philosophical point of view, for the recognition of segregate genera. Thus, the people who were instrumental in causing the splitting, never justified their actions on theoretical grounds (Robinson, 1906; Anderson, 1940; Bartlett, 1940). Overall, the splitting tendency caused the loss of a generic concept (Bremer, 1976) and nomenclatural confusion (Arkell & Moy-Thomas, 1940; Greenman, 1940). This was followed by disagreement that became manifested as unstable classifications and probably contributed to distaste among biologists for taxonomy (Vernon, 1993).

Numerical taxonomy and phenetics

Further distaste may have been fuelled by classifications increasingly being interpreted as being based on the 'probable phylogeny' (Cain, 1956; Michener & Sokal, 1957; Bremer, 1976; Humphries, 1979), an interpretation that was not unanimously accepted. Some considered that 'phylogeny' could not be known and where it was known, it would be inadequate for classification since it made use of only a few characters (Gilmour, 1961; Gilmour & Walters, 1964). Others did not believe that classifications could express phylogeny (Simpson, 1945; Cain, 1956; Michener, 1957). Resistance to making phylogenetic evaluations part of classifications made way in the early 1960s for numerical taxonomy or phenetics (Funk & Stuessy, 1978). Phenetics, based on numerical evaluation of the affinity between taxonomic units or the ordering of these units into taxa (Sokal & Sneath, 1963; Sneath & Sokal, 1973), removed the need for any *a priori* selection of characters as more important (Davis & Heywood, 1963; McNeill, 1979) and was therefore considered to be more objective (Stevens, 1984). But objectivity was not prioritised by all. Michener & Sokal (1957) compared the outcome of the phenetic method and the phyletic method on a classification of bees. The phenetic method was based on determining generic rank by means of objective cut-off points in the form of horizontal lines drawn across a dendogram and the phyletic method was based on "assumed or known phyletic relationships" (Michener, 1957: 160). Despite finding that the two methods produced largely similar classifications, Michener (1957) famously rejected the use of the phenetic method on the basis of his intuition and zoological tradition, which

placed more weight on 'phylogeny'. One of the early studies on plants employing numerical methods saw the subsuming of satellites into a broader defined *Salvia* (El-Gazzar & al., 1968). Indeed, numerical methods often showed that many contemporary genera were typologically founded (Walters, 1986).

Cladistics

During the same period Hennig (1950, 1966) formulated his theory on cladistics, introduced the concept of monophyly and put homology into analytical context. Cladistics was transformed from a theory into a methodology by Platnick, Patterson and others (Hull, 1984; Linder, 1988) and was accompanied by alternative methods to phylogeny inference, such as Wagner's (1961) ground plan/divergence approach. Koponen (1968) published the first botanical cladistic study, but in general phylogenetics had much less effect upon classification in botany than in zoology in the early days (Bremer, 1976; Bremer & Wanntorp, 1978). Pheneticists argued that cladistics, a method for phyletic tree construction, was an activity separate from that of producing a classification (McNeill, 1979). Others (Bremer & Wanntorp, 1978; Funk & Stuessy, 1978) realised that the inference of phylogenies and the construction of classifications could logically and practically go hand in hand as congruent activities. In the 1980s cladistics gained widespread acceptance as a method in plant taxonomy (Linder, 1988). This made way for arguably the most important conceptual shift in the history of generic delimitation: monophyletic genera.

Numerical taxonomy and cladistics do not reflect conceptual shifts, in terms of that genera should represent 'natural' as opposed to 'artificial' units. However, there has been a shift in what 'natural' means. Whereas 'naturalness' was previously conveyed by morphological correspondence, the advent of cladistics meant that it could be conveyed through synapomorphy. Systems recognising monophyletic genera have been considered superior to those consisting of 'traditional genera' through the avoidance of (1) core genera, usually large, paraphyletic groups with many associated satellites, e.g., *Veronica* L. before Garnock-Jones & al. (2007) (Funk, 1985), and (2) artificial genera, groups quite unrelated through common descent (Humphries, 1979; Funk, 1985). This was indeed true for the systems with monophyletic genera established by Bremer (1976), Weston & al. (1984), Funk (1985) and Anderberg (1986).

Data development

Our historical tour lacks one important factor: different data types employed at different times. Morphology has been used throughout—it is basic to how we perceive nature. Its use for classifying plants goes back to ancient times, e.g., to the writings of Theophrastus (ca. 300 B.C.). Perhaps it is precisely this ancient and widespread use of morphological data that has contributed to the view that classifications based thereon are descriptive and only semi-scientific (Constance, 1957).

Eighteenth century botanists, e.g., Linnaeus and Jussieu, defined genera on outstanding features. Their generic divisions were often monothetic, with an emphasis on reproductive features (Stafleu, 1971; Sloan, 1972; Frodin, 2004). In contrast, Adanson (1764) followed Tournefort's lead and produced classifications based on a totality of characters (Humphries, 1979). The sole use of gross morphology, with the gradual incorporation of vegetative anatomy and palynology into botany, remained customary until the 1920s when a suite of cytological, physiological, ecological, genetic, embryological and chemical data became available (Hagen, 1984; Vernon, 1993; Frodin, 2004). Effectively these are all sorts of morphological data, but their incorporation revealed new patterns and in particular the study of chromosomes was considered to reveal 'true' genetic relationships, since it more closely represented the germplasm (Constance, 1957; Vernon, 1993). To be sure, botanical systematics was suffering from a general paucity of data compared with zoological systematics, where embryology, palaeontology and anatomy were providing evolutionary

insight (Bather, 1927; Stevens, 1984). In botany, there had long been a desire to break up polythetic groups, but information on how this may best be done had been lacking. Formerly obscure, but potentially good characters in restricted groups provided the information necessary for the splitting of larger groups (Babcock, 1947; Constance, 1957). For instance, improved knowledge of cupular morphology and anatomy resulted in the removal of *Lithocarpus* Blume *s.l.* from *Quercus*, with some further dividing of Asian taxa (Frodin, 2004), and the dismantling of the very large *Eupatorium* L. (Asteraceae) (King & Robinson, 1970). Physiological studies revealed differences in photosynthetic modes (Moss & al., 1969; Pearcy & Troughton, 1975) that reinforced suggestions based on gross morphology (Webster, 1967; Frodin, 2004) of renewed recognition at the generic rank of *Chamaesyce* S.F. Gray (Koutnik, 1984, 1987) and of the segregation of several smaller genera from *Cyperus* L. (Goetghebeur, 1986; Bruhl, 1995). New data provided more information in some groups than others. In Fabaceae and Asteraceae most cytological studies confirmed existing classifications (Anderson, 1937; Stebbins, 1956), whereas in Poaceae, that lacks many of the floral characters used in other families, cytological data revealed many 'intergeneric' hybrids in the tribe *Hordeae* and led to the merging of ten genera into one (Stebbins, 1956). Even contemporary writers saw the drastic changes being caused by the incorporation of new data, especially cytological (Constance, 1957), and in hindsight new kinds of data have each been successively touted as a systematic panacea, in part responsible for successive systematic rearrangements during the 20th century (Stevens, 2000). Disagreement among the patterns displayed by different kinds of data would provoke renewed study of the characters in question, in an act of reciprocal illumination that has become so central to taxonomic work.

In the 1980s chemical data were taken to a new dimension. Early work in vertebrates, in which the idea that primary protein structure could contain evolutionary information was tested (Zuckerkandl & Pauling, 1965), showed a high degree of congruence between amino acid sequences, fossil evidence and classical ideas on phylogeny (Boulter & al., 1979). In plants, the absence of a continuous fossil record made the use of amino acid sequence data as a potentially objective aid for phylogeny reconstruction particularly welcome (Boulter & al., 1970, 1972). Widespread application of nucleotide sequence data for phylogeny reconstruction, or indeed for the study of genera, was not achieved until well after their initial suggested use. This lag is more likely to have been technically than philosophically founded, since incorporation of molecular data was dependent upon the development of numerical and cladistic methods of analysis, computational technology and ease of DNA sequencing. Molecular data (now also direct DNA and RNA sequences) is today widely used to investigate the nature and inclusiveness of genera, albeit not without criticism (e.g., Stace, 2005; Farjon, 2007), perhaps some of which stems from the perception that studies employing molecular data are causing excessive generic redelimitation (e.g., Frodin, 2004; Barrett & al., 2005; Stace, 2005; Farjon, 2007). We investigate this contention in detail below.

Current trends in delimitation of plant genera

Current taxonomic literature abounds with cases of generic delimitation based on molecular phylogenetic analyses. We have shown above how, in the past, addition of new suites of data have caused major taxonomic rearrangements. We have also shown that not only changes in data, but also conceptual changes, influence generic delimitation. To gain a better understanding of what drives changes in generic limits today, we reviewed the literature for recent cases of generic delimitation in vascular plants. In particular, we wanted to test the notion that the addition of nucleotide sequence data is causing a current surge in generic (re)delimitation. If this is true, is this simply due to a shift in data or does it reflect a conceptual shift?

We searched four leading systematic journals (*Australian Systematic Botany, Plant Systematics and Evolution, Systematic Botany* and *Taxon*) for papers on generic delimitation, starting in mid 2007 and going back to 1998. These journals were chosen as they are

prominent in the field of plant systematics and have broad international coverage, being published in three continents (Australia, Europe, North America). For each paper on generic delimitation found we asked: (1) What data are being used? (2) Are genera getting smaller or larger? (3) What criteria are the new generic limits based on? (4) Is there an explicit justification, from a theoretical/conceptual point of view, for the generic limits being drawn?

We found 194 papers on generic delimitation published in the past (almost) ten years (Appendix). Studies simply confirming monophyly of genera were ignored, since we were interested in cases of generic realignment. Placement of species (description of new species), causing a change in generic size, represents changing concepts of species and not genera. These studies were also ignored unless species were transferred for a particular reason (e.g., to maintain monophyly or morphological homogeneity) because the underlying conceptual shift is then related to the genus. Five of the papers found were entirely theoretical and three included duplicate cases of generic delimitation (i.e., cases had to be scored differentially). We encountered several papers in which new generic limits were implied, but where no formal taxonomic changes were made. These were excluded from the analysis, since until formal taxonomic changes have been made, the opinion of the authors might change. In ten cases 'implied' generic delimitations were included, because they were accompanied by explicit statements concerning forthcoming changes, with a reference to formalisation underway ('in press' or with reference to the author[s]). Twelve of the studies were on fossil genera and these were also removed, since they can only ever be form genera. This resulted in 180 cases of generic delimitation forming the basis for the following analysis and discussion.

What data are being used?

We counted the cases in which molecular data were used and those in which only morphological data were used. Molecular data were included in 113 cases and 67 cases were based on morphological data alone. We separated the data into two five-year blocks, 1998–2002 and 2003–2007, and found that in the first five years 35 cases were based exclusively on morphological data and 32 cases included molecular data (Fig. 2A). In the second five-year period, a similar number of cases were based on morphological data alone (32), whereas the number of cases including molecular data almost tripled (81). The proportion of cases in which molecular data are used is significantly higher in the second five-year interval than in the first five-year interval (Pearson's chi-square test, $P < 0.01$, d.f. = 1). Together, these figures indicate that incorporation of molecular data is stimulating renewed research interest in generic delimitation and that it may be causing generic realignment.

Are genera getting smaller or larger?

We counted the number of cases where generic delimitation resulted in larger genera versus those resulting in smaller genera. The category 'smaller' includes description of new genera and also monotypic genera. In 22 of the included cases generic realignment was the result of the transfer of species from one genus to another, leaving the overall generic sizes unchanged. These cases were therefore excluded from this part of the analysis. On the whole, genera seem neither to be getting smaller nor larger (80 versus 78, respectively). We evaluated these figures against the figures for 'morphological' and 'molecular' data (above) to see whether the sort of data used influences eventual generic sizes. Larger genera mainly result from studies including molecular data and significantly fewer studies based on morphological data alone result in recognition of larger genera (Pearson's chi-square test, $P < 0.01$, d.f. = 1) (Fig. 2B).

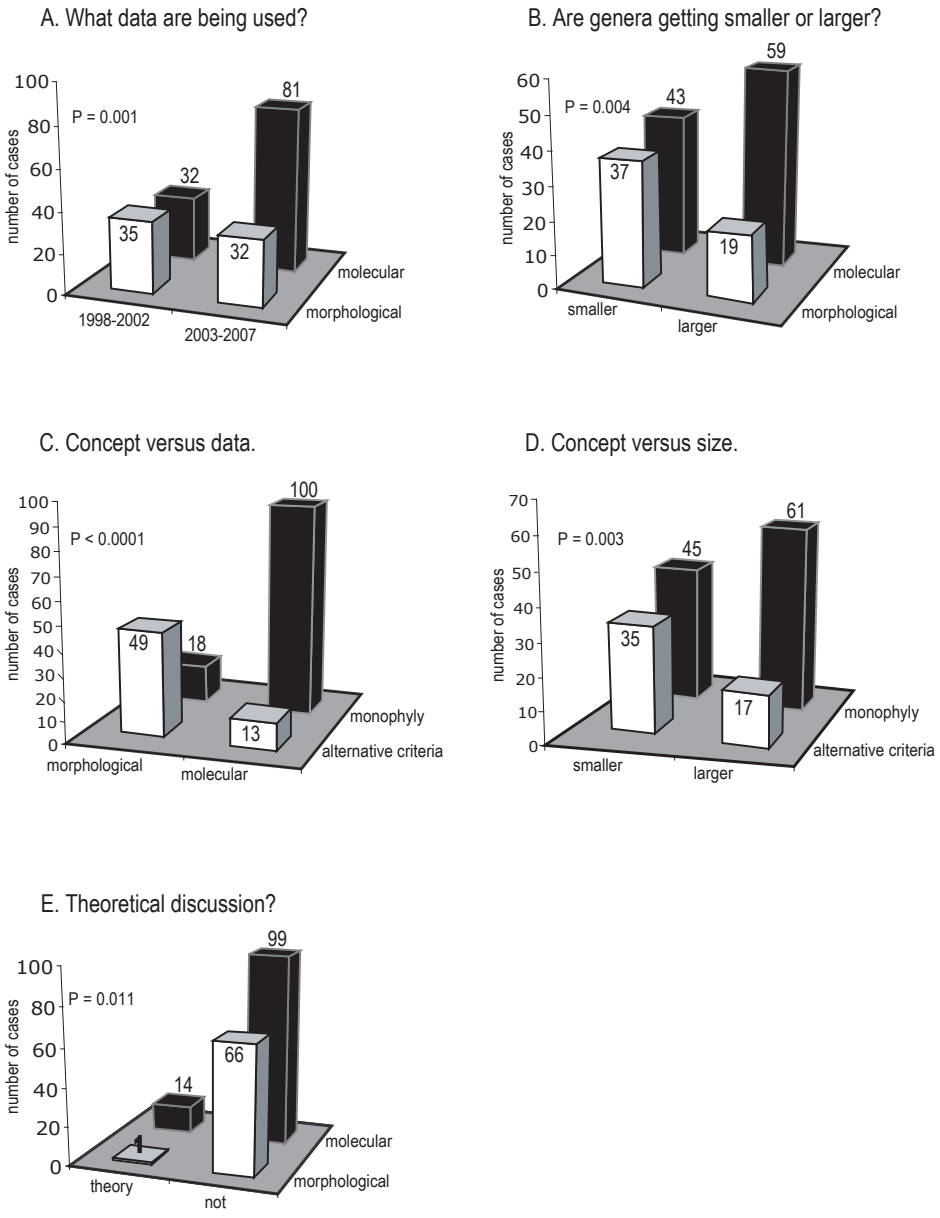

Fig. 2. Contemporary approaches to generic delimitation: relationship among genus sizes, data, criteria and theoretical justifications (concepts). *P*-values refer to Pearson's chi square test (A–D) and Fisher's exact test (E). A, number of cases in which molecular data were included, versus those employing morphological data alone, split into two five-year blocks. B, number of cases in which smaller genera are recognised, versus those in which larger genera are recognised, split depending on the kind of data used. C, number of cases in which monophyly was used as a criterion for generic delimitation versus number of cases based on alternative criteria, split depending on the kind of data employed. D, number of cases in which monophyly was used as a criterion for generic delimitation versus number of cases based on alternative criteria, split depending on whether larger or smaller genera are recognised. E, number of case in which generic delimitation was accompanied by a theoretical discussion versus those in which there was no theoretical discussion, split depending on the kind of data used.

What criteria are generic limits based on?

We listed the explicit criteria stated by the authors and tallied the number of times each criterion or set of criteria were used (Table 1). Just as we used inclusion of molecular data to represent a shift in data, we used 'monophyly' versus 'alternative criteria' to represent a shift in concept. Overall, monophyly (usually in combination with other criteria, such as diagnosability and number of nomenclatural changes; Table 1) was used in 118 cases and 62 cases were based entirely on alternative criteria (most commonly morphological similarity). We found a significant relationship between criterion and data type, such that monophyly is mostly used in conjunction with molecular data and most cases employing morphological data alone use alternative delimitation criteria (Pearson's chi-square test, $P < 0.01$, d.f. = 1) (Fig. 2C). Similarly, there is a significant relationship between criterion and changes in genus size, such that larger genera are mostly recognised under the criterion of monophyly and very few cases in which alternative criteria are used, lead to the recognition of larger genera (Pearson's chi-square test, $P < 0.01$, d.f. = 1) (Fig. 2D). Analysed together, the kind of data employed and the criterion used influence genus sizes (Pearson's chi-square test, $P < 0.01$, d.f. = 3) (Table 2).

Is there an explicit justification, from a theoretical or conceptual point of view, for the generic limits being drawn?

No, there is not. Regardless of whether molecular or morphological data are being used a generally low proportion of cases are explicit about the underlying justifications for the new generic limits being drawn, although a significantly higher number of cases using molecular data justify their actions (13% versus 1.4%, Fisher's exact test, $P = 0.01$) (Fig. 2E).

Concept versus data in delimitation of plant genera

We demonstrate the presence of a relationship in contemporary generic delimitation between the use of molecular data, the criterion of monophyly and broadly construed genera on the one hand and morphological data, alternative delimitation criteria and narrowly construed genera, on the other. Historically, the development of a 'natural' classification in both botany and zoology shows a complex interaction between the type of information available, the perception of the patterns and metaphysical ideas (Stevens, 1984). In other words: interplay between data and concept, just as we found in the present meta-analysis (Fig. 2B, D; Table 2). It is more interesting, however, to disentangle the effect of one of these factors on prevailing genus sizes from the effect of the other. Over the past 300 years new types of data have been introduced twice (Fig. 1): the first introduction coincided with the splitting era of the last century and the second introduction appears to be leading to a renewed recognition of larger genera. Conceptual shifts have occurred several times (Fig. 1), only one of which appears to have had a direct effect on prevailing genus size in the absence of a change in data: the shift from smaller to larger genera in the 18th and 19th centuries was driven by the quest for generic classifications to remain stable and memorable.

At a first glance, then, it would appear that changes in data drive changes in prevailing genus size. However, new data do not come with an *a priori* method by which they

Table 1. Explicit criteria used in 180 cases of generic delimitation published 1998–2007, listed using the phrasing of the authors. The use of '/' to separate criteria means 'or'; separation of criteria with a ',' signifies that criteria have been ranked by the authors and have been listed here in descending priority; separation of criteria with 'AND' signifies that no priority was assigned to any criterion.

Criteria	[illegible]	[illegible]	[illegible]
Morphological similarity/isolation	27	21	48
Monophyly	20	26	46
Monophyly, morphology	7	21	28
Monophyly AND morphology	3	14	17
Morphological and molecular (relatedness) isolation/similarity	1	10	11
Monophyly, number of nomenclatural changes	1	3	4
Monophyly, stability (node support), morphology	0	5	5
Monophyly, number of nomenclatural changes, diagnosability	0	2	2
Monophyly, molecular relatedness	2	0	2
Monophyly, morphological homogeneity	0	2	2
Monophyly, stability (node support)	0	2	2
Monophyly, number of nomenclatural changes in relation to how charismatic or economically important a genus is	0	1	1
Monophyly, stability (node support), size of genus (not too small), biological equivalence of units	0	1	1
Nomenclatural stability, Monophyly	0	1	1
Monophyly AND morphology, stability	0	1	1
Monophyly, avoidance of monotypes	1	0	1
Monophyly, avoidance of monotypes, morphology	0	1	1
Monophyly AND morphology, molecular relatedness	1	0	1
Monophyly, previous taxonomic transfer, stability (node support)	1	0	1
Molecular relatedness	1	0	1
Monophyly, avoidance of monotypes, minimise number of genera	0	1	1
Hybridisation between two species, morphology	1	0	1
Monophyly, information content (> in one large genus)	0	1	1
Reduction in number of poly-/paraphyletic genera but retain some due to: no. of nomenclatural changes, diagnosability	1	0	1
TOTAL	67	113	180

Table 2. Contingency table for number of cases in which various combinations of data and concept lead to smaller or larger genera. The proportions of cases resulting in smaller or larger genera, depending on data and concept, is significantly different from those under the null hypothesis, which states that the kind of data and concept does not influence genus sizes (Pearson's chi-square test, $P = 0.005$, d.f. = 3).

	Smaller	**Larger**	Row total
Monophyly/morphological	11	6	17
Monophyly/molecular	34	55	89
Alternative criteria/morphological	26	13	39
Alternative criteria/molecular	9	4	13
Column total	80	78	

should be analysed (Stevens, 1987, 2000) and interpreted as a generic classification. We found that studies relying on morphological data alone relied mostly on morphological similarity to guide generic delimitation (Fig. 2C; Table 1), but there is no reason why new groups that share new characters must be recognised at the generic rank. For example, anatomical data were in widespread use by the end of the 19th century (Constance, 1957), and although they no doubt led to modification of current systems, they did not cause large scale reshufflings at that time. In fact, the description of numerous smaller genera during the last century coincided with a conceptual shift from study focused on the generic rank to study at the specific rank and below. This shift no doubt reinforced emphasis on differences rather than similarities. Likewise, the widespread use of molecular data in studies of the generic rank today is associated not only with a return to a renewed recognition of larger genera (Fig. 2B) but also with the delimitation of genera on the basis of monophyly (Fig. 2C). This strongly suggests that changes in generic delimitation practice, although they may include the use of new sources of data, are conceptually founded and in line with contemporary research trends. Finally, the technological advances that have allowed widespread incorporation of molecular data into taxonomic studies (automated sequencing that facilitates gathering large amounts of DNA sequence data and computational capacity for their analysis) have also facilitated a return to a global approach to the study of plant genera.

Translating a phylogeny into a classification and the pursuit for optimal genera

Although molecular phylogenetics is increasingly contributing to generic classifications, there is no consensus on how phylogenies may best be translated into a classification (Barkley & al., 2004; Pfeil & Crisp, 2005; Entwistle & Weston, 2005; and see Liede-Schumann & Hartmann's (2009) comments on Klak & al.'s (2007) classification of the Mesembryanthemoideae). Guidelines pertinent to the incorporation of phylogenies and (generic) classifications have been published by several authors (Table 3). In the strict Hennigian system, classifications should meet two criteria: all taxa should be monophyletic and the classification should be constructed in such a way that it can be read directly off the cladogram (Funk, 1985). In practice, both may be difficult to realise. Of major concern is how to discern which clades should be recognised at the generic rank (e.g., Backlund & Bremer, 1998; Orthia & al., 2005). We advocate an approach, similar to that of Bentham and that can be traced back through the work of Linnaeus and to folk taxonomies: we prefer to recognise larger monophyletic groups at the generic rank, over several, small monophyla. In our work in the danthonioid grasses

(Linder & al., submitted), perhaps a strict adherence to this statement would mean equating the entire subfamily with the

Table 3. Published guidelines on translating a phylogeny into a (generic) classification.

Hennig, 1966	**Funk, 1985**	**Oberwinkler, 1994**	**Backlund & Bremer, 1998**
1. Monophyly. 2. Classification should be able to be read off the cladogram. 3. Each group should have hierarchial rank as determined by its geological age of origin.	1. Monophyly. 2. Minimal disruption of present classification.	1. Monophyly. 2. Before a monophyletic group is split into two or more monophyla, the improvements (easier to handle) should be evident. 3. Avoid monotypic genera. 4. Before genera are united it must be shown that they are sister groups, and the improvements for taxonomic purposes must be evident. 5. Paraphyletic genera should be split into monophyletic taxa.	Principles of classification: 1. Primary principle of monophyly; 2. Secondary principles[1] of - stability; - phylogenetic information(or minimise redundancy); - support for monophyly; - ease of identification.
Barkley & al., 2004[2]	**Pfeil & Crisp, 2005**	**Entwistle & Weston, 2005**	**Stuessy, 2009a, b[3]**
1. Classifications should be maximally predictive, achieved through descent with modification. …. 13. Science should not be constrained by nomenclature, but neither should nomenclature constrain science. "It is important that a scientist be allowed to decide what is important in his/her classification" [p. 158].	1. Monophyly. 2. Genera should be defined by robust clades, in order to maximise the chance of long-term stability. 3. Maximised use of previously applied names and the number of species that remain in the genus within which they have traditionally been placed.	1. Named taxa should be monophyletic based on current reliable evidence. 2. Minimise taxonomic change. 3. Change is more acceptable in groups that are not 'charismatic', not economically important, or do not have a substantial 'interest group'.	1. Select monophyletic group. 2. Code and weight evolutionarily important characters. 3. Cladistic analysis. 4. Develop nested hierarchy based on branching pattern. 5. Determine apomorphic information of each branch relative to the total apomorphic information in the tree. 6. Modify nested hierarchy based on apomorphic information content of each group.

[1] Not listed in any particular order, but will have different weight in different plant groups.

[2] Refers to integrating traditional nomenclature and phylogenetic classification, not genera *per se.*

[3] Explicit phyletic (evolutionary) classification.

generic rank (*Danthonia* D.C.). As this would have several practical disadvantages today, including vast nomenclatural disruption, we do not follow this route. However, where possible we have opted for broadly construed genera (e.g., *Pentameris* Beauv. s.l. and *Rytidosperma* Steud. s.l.) (Humphreys & al., submitted; Linder & al., submitted) as opposed to recognising the smallest group above the species requiring a name, an approach more in the spirit of Tournefort. Given topological uncertainties present in molecular phylogenies we contend that this will yield a more stable classification, robust to minor shuffling at lower ranks. A system with larger genera also has the practical advantage that one can be relatively confident about the genus identity and need only worry about keying out the species (Robinson, 1906). The

linguistic advantage of large genera over several smaller genera is clear from folk taxonomies (Bartlett, 1940; Raven & al., 1971; Berlin & al., 1973). Too fine generic segregations ignore evidence that too many names for very similar things cannot be borne in mind and will eventually fall into disuse. This leads on to the criterion of 'memory', which was used by Linnaeus as well as Bentham to ensure that a working taxonomist could memorise the genera within a system. However, somewhere along the course of history it seems that this may have been misinterpreted as meaning 'memorising all the species of a genus' and leading to abandonment of larger genera on the basis that they were 'difficult to work with and to memorise'.

An alternative approach to determining rank is to recognise only groups of equivalent age (Avise & Johns, 1999; Orthia & al., 2005; Avise & Mitchell, 2007; Dubois, 2007; Linder & al., submitted), referred to as "absolute ranking" by Hennig (1966: 154), but using relative ages within the group of interest rather than absolute ages across phylogenetically distant groups. This has been discussed in the past by Funk (1985), Funk & Stuessy (1978) and Stevens (1987) and has been applied to the reclassification of birds (Sibley & Ahlquist, 1986) and primates (Goodman & al., 1998). The attractiveness of this approach today is its renewed achievability, given molecular dating techniques, even if uncertainty of node ages must to be taken into account if extrapolated for use in classifications. Use of age as a criterion for generic delimitation means that genera may represent comparable units. If genera do not represent comparable units their use as such outside the systematic community (Knapp, 2008; Mike Crisp, pers. comm) may lead to invalid inferences.

In establishing, and even looking for, consensus guidelines in how to best establish a generic classification in a phylogenetic framework, we are leaving an era of supposed consensus reached through a 'fair amount of agreement' among publishing taxonomists (Anderson, 1940). This 'fair amount of agreement' can no doubt be attributed to the way we have been selected to think (intuition) (Anderson, 1957; Atran, 1990; Stevens, 2000) and to the fundamental sorting mechanism described by Jeffrey (1987). In a shift from transcendentalism, the valuing of intuitive and spiritual processes (James, 2009), into empiricism, we hope that stable generic classifications will be achieved by adhering to the principles of Bentham in the sense of *what to delimit* (large genera) and Hennig in the sense of *how to group* (empirical evidence rather than obscure consensus).

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Appendix. Literature sources for the survey of contemporary generic delimitation.

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Chapter 2.

A PLASTID TREE CAN BRING ORDER TO THE CHAOTIC GENERIC TAXONOMY OF *RYTIDOSPERMA* STEUD. S.L. (POACEAE)

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"There is probably no other family of flowering plants in which cytogenetic evidence will do more to reveal the artificiality of conventional taxonomic treatments than the Gramineae. As Dr. Edgar Anderson has said (oral comm.), grasses are "streamlined," and possess a minimum of the elaborations of form which help taxonomists to make distinctions in other families."

Stebbins (1956, p. 241)

Abstract

Rytidosperma s.l., wallaby grasses and allies, is in dire need of a single, unanimously accepted generic taxonomy. Motivated by the desire to establish a generic classification that complies with phylogeny, we investigated how much phylogenetic signal is contained within a plastid (cpDNA) tree, given that the nrDNA tree (ITS) was uninformative and that a phylogenetic hypothesis based on a single genome may not be reliable. We find that the plastid tree is significantly different from a morphological cladogram and show that this is the result of homoplasy in the morphological dataset. Treated individually, several morphological characters fit the plastid tree very well. Similarly, we find a good fit of the plastid tree with ecological and distribution characters and with biogeographical patterns in the Southern Hemisphere. We conclude that a significant level of the species phylogeny is resolved by the plastid tree and are confident it can form a sound basis for a reconsideration of generic limits. None of the currently recognized seven genera in the Rytidosperma clade is monophyletic. Therefore, we propose combining the segregate genera in Australasia within a broadly construed Rytidosperma, including all the species from Australia, New Guinea, New Zealand and South America.

Introduction

A number of prerequisites for taxonomic chaos are fulfilled by the grass genus *Rytidosperma* s.l.: substantial morphological variation, an intercontinental distribution and a relatively large number of species. Indeed, for the past 40 years the generic delimitation of the 74 species in *Rytidosperma* s.l. has been confused. Until the 1960s all of the then recognised species were included in the genus *Danthonia* DC widespread in temperate regions of the Southern Hemisphere and extending to North America and Eurasia. Zotov (1963) started the segregation of *Rytidosperma*-like species from *Danthonia* with the description of three genera in New Zealand: *Notodanthonia*, *Pyrrhanthera* and *Erythranthera*. A decade later Blake (1972) transferred all of the Australian species to Zotov's *Notodanthonia*. In South America, segregation of Danthonia went down a different route. Nicora (1973) realised that Zotov's *Notodanthonia* was equivalent to Steudel's (1854) genus *Rytidosperma* and transferred six Andean species of *Danthonia* to *Rytidosperma*, thus reviving Steudel's (1854) concept of a southern entity distinct from the now primarily northern genus *Danthonia*. Soon thereafter Connor and Edgar (1979) made the appropriate synonymisations of *Notodanthonia* with *Rytidosperma* for the species in New Zealand. What was then to follow illustrates the confusion surrounding these grasses and highlights the danger of limiting study of a group to only a portion of its geographical range or taxonomic scope (Bentham, 1858). Veldkamp (1980), working on the New Guinean species, called for the conservation of what he considered a much more established name, *Notodanthonia*, over Rytidosperma. Jacobs (1982) in Australia opposed this, while at the same time expressing his dissatisfaction regarding the separation of *Rytidosperma* from *Danthonia*. Clayton and Renvoize (1986) suggested that *Erythranthera*, *Karroochloa* Conert and Türpe and *Merxmuellera* Conert be included in *Rytidosperma*, thereby extending the concept of *Rytidosperma* to species from Africa for the first time. None of the concepts of these segregate genera was ever adopted in Australia – although the species there were clearly allied – where a broad concept of *Danthonia* remained (Beadle et al., 1982; Jacobs, 1982, 1993; Scott and Whalley, 1982; Simon, 1993; Walsh and Entwistle, 1994). Finally, in the mid-1990's cladistic methodology was used to draw up a new generic system for all of the Australasian species (Linder and Verboom, 1996; Linder, 1997). *Notodanthonia* and *Rytidosperma* (including Pyrrhanthera and *Erythranthera* and the New Guinean genus *Monostachya* Merr.) were redelimited and two new genera, *Austrodanthonia* Linder and *Joycea* Linder, were erected to accommodate the remaining species. Also in this analysis an affiliation to the African *Karroochloa* was clear but cytological differences justified its continued separation. An association with *Karroochloa* was eventually confirmed by molecular phylogenetic analyses, following which *Notodanthonia*, *Rytidosperma*, *Austrodanthonia* and *Joycea* in Australasia, *Karroochloa*, *Schismus* and *Tribolium* in Africa, and a handful of montane species belonging to *Danthonia* and *Merxmuellera*, were united in the "Rytidosperma clade" (Barker et al., 2000). Of course, definition of this informally named clade did not address the taxonomic chaos at the generic rank, which remains dire. The New Zealanders continue to recognise a broad *Rytidosperma* (with *Pyrrhanthera* segregated) (Edgar and Connor, 2000), a concept that holds in South America (Baeza, 1996, 2002) and New Guinea (Veldkamp, 1993, 2004), whereas in Australia Linder and Verboom's (1996) generic concept has gained widespread acceptance and is adopted also beyond the scientific community. The taxonomic history of the African genera *Karroochoa*, *Schismus* and *Tribolium* has been less chaotic. Cladistic analysis of morphological data confirmed that each genus was reciprocally monophyletic with the inclusion of *Urochlaena pusillum* Nees in *Tribolium* (Linder and Davidse, 1997), but recent analyses have revealed that these genera do not correspond to monophyletic groups on molecular phylogenetic grounds (Verboom et al., 2006).

A unanimously accepted generic classification is an imperative for sound taxonomy and unambiguous communication. The existence of more than one working taxonomy may seriously hamper communication because it opens the possibility of confusion and error, obscuring the information that can be conveyed with a good classification. In a group that includes species of economic value disagreement among taxonomists will have considerable consequences beyond the scientific community (see Brickell et al., 2008). In Australia, the wallaby grasses, Austrodanthonia, include several species that are important pasture grasses (Lodge and Whalley, 1989; Lodge and Groves, 1990). Other Austrodanthonia species are used in landscaping and revegetation projects, as midrow plants for citrus and grapes (Jessop and Giddings, 2006) and in addition several of the *Rytidosperma*-affiliated species occur as weeds well beyond their native range (e.g. *Austrodanthonia pilosa*, *Schismus barbatus* and *S. arabicus* in North America (Darbyshire, 2003)). An unfortunate example of how a chaotic taxonomy may be perpetuated as error and cause confusion among end users of taxonomy occurs in the recently published Manual of Grasses for North America (Darbyshire, 2007), in which the same species are referred to as *Austrodanthonia* in the introduction and key and *Rytidosperma* in the species description.

One solution to defining a sound generic classification is to use a phylogenetic hypothesis as a framework, such that genera are based on 'natural groups' in evolutionary terms (Kornet, 1994; Oberwinkler, 1994) and so that monophyletic genera may be recognised (Hennig, 1966; Funk, 1985; Backlund and Bremer, 1998). The cladograms of Linder and Verboom (1996) and Linder and Davidse (1997), which support the segregate genera, lack node support, do not include any of the South American species and the former is based on limited taxon sampling. There is an increasing trend toward the use of nucleotide sequence data in taxonomic studies at the generic rank (Humphreys and Linder, 2009). *Danthonioideae* is no exception: a string of recent molecular phylogenetic studies have addressed generic delimitation of certain groups (*Cortaderia*: Barker et al., 2003; African members of the Rytidosperma clade: Verboom et al., 2006; *Pentaschistis* and allies: Galley and Linder, 2007) or have assessed generic limits in the subfamily as a whole (Pirie et al., 2008). However, none of these studies has provided resolution of the Rytidosperma clade that is informative enough to serve as a guideline for a generic classification. To complicate matters further, several studies in the Danthonioideae have revealed well supported conflict between nuclear and plastid (chloroplast) gene trees (Barker et al., 2007; Pirie et al., 2008, 2009), which has been attributed to ancient hybridisation events (Pirie et al., 2009). Here we increase both taxon and character sampling of the Australasian and South American members of the *Rytidosperma* s.l. and test the usefulness of a single genome phylogeny (cpDNA) for bringing order to a chaotic generic classification, against a background of morphological, distribution and ecological data.

Methods

Taxon sampling

Nomenclature follows Linder and Verboom (1996) (Australasian species), Baeza (1996) (South American species) and that used by Linder and Davidse (1997) (African species). We sampled globally, expanding on the existing datasets of Barker et al. (2000, 2003, 2007), Verboom et al. (2006) and Pirie et al. (2008). Main obstacles to achieving complete taxon sampling were geographical inaccessibility and rarity or possible extinction of species. Species for which we were unable to obtain fresh material, along with the aforementioned reasons, are listed in Table 1.

Table 1. Listing of unsampled species and the reasons preventing their sampling.

Taxon	Country	Locality	Reason unsampled (A)/Reason not collected by the authors (B)/Status (C)	Formally recognised threat status	Herbarium extraction tried? (A)/Material (B, C)	Collector other than authors
A. Species unsampled in the study						
Schismus inermis (Stapf) C.E.Hubb.	SA	Bredasdorp Flats	Couldn't find it		no	
Austrodanthonia bonthainica (Jansen) H.P.Linder	SE Asia	Celebes (Bonthain)	Politically inaccessible		no	
Rytidosperma craigii (Veldk.) H.P.Linder	SE Asia	W Sepik Prov., Papua New Guinea	Politically inaccessible		no	
Rytidosperma dendeniwae (Veldk.) H.P.Linder	SE Asia	Northern Prov., Papua New Guinea	Politically inaccessible		no	
Rytidosperma javanicum (Phwi ex Veldk.) H.P.Linder	SE Asia	Java, Malang	Politically inaccessible		no	
Rytidosperma mamberamense (Jansen) Connor & Edgar	SE Asia	New Guinea, Irian Jaya	Politically inaccessible		no	
Rytidosperma montis-wilhelmii (Veldk. & Fortuin) H.P.Linder	SE Asia	Irian Jaya and W Highlands Prov., Papua New Guinea	Politically inaccessible		no	
Rytidosperma nardifolium (Veldk.) H.P.Linder	SE Asia	Central Prov., Papua New Guinea	Politically inaccessible		no	
Rytidosperma nudum (Hook.f.) Connor & Edgar	NZ	Ruahine and Tararua Ranges, North Island	Couldn't find it. (Rare. Does not set seed. (H. Connor & K. Lloyd pers. comm.))	At Risk/Range Restricted[1]	yes	
Rytidosperma viride (Zotov) Connor & Edgar	NZ	southern North Island and NW Nelson, South Island	Couldn't find it. (Rare. Does not set seed. (H. Connor & K. Lloyd pers. comm.))		yes	
Rytidosperma tenue (Petrie) Connor & Edgar	NZ	Nelson and Westland, South Island	Couldn't find it. (Rare. Does not set seed. (H. Connor pers. comm.; Connor, 1988))	Data Deficient[1]	no	
Rytidosperma horrens Connor & Molloy	NZ	Lake Ohau area, South Island	Rare, geographically difficult access (helicopter)	Data Deficient[1]	no	
Austrodanthonia remota (D.I.Morris) H.P.Linder	AU	Hibbs Pyramid, on island W of Tasmania	Rare, geographically difficult access (island)	Rare[2]	no	
Austrodanthonia biannulare (Zotov) H.P.Linder	NZ	Southern North Island (to Auckland) and northwest South Island	Time limitations prevented visiting this area		yes	
Notodanthonia nigricans (Petrie) Zotov	NZ	Tararua and Rimutaka ranges, North Island; west of the Main Divide, South Island	Time limitations prevented visiting area (couldn't find it in Tararua)		yes	
Rytidosperma sorianoi Nicora	Arg	Prov. Neuquén	Time limitations prevented visiting this area		no	
B. Species not collected by the authors, but for which material was provided by colleagues						
Austrodanthonia induta (Vickery) H.P.Linder	AU	From southern Qld, west to the Vic-S.A. border, and in Tas.	Never found it		silica	N. Walsh
Austrodanthonia acerosa (Vickery) H.P.Linder	AU	W.A.	Time limitations prevented visiting this area		silica	T. Macfarlane
Austrodanthonia occidentalis (Vickery) H.P.Linder	AU	W.A.	Time limitations prevented visiting this area	Poorly Known[2]	silica	T. Macfarlane
Austrodanthonia richardsonii (Cashmore) H.P.Linder	AU	N.S.W., Vic., S.A.	Never found it		seed	USDA
Rytidosperma paschale (Pilg.) C.M.Baeza	Chl	Easter Island	Time limitations prevented visiting this area		cultivated plant	G. Zizka
Rytidosperma petrosum Connor & Edgar	NZ	Wellington, North Island; Nelson, South Island; plus islands off the NZ coast	Couldn't find it	At Risk/Range Restricted[1]	DNA extraction	J. Keeling, R. Gardner & P. de Lange
Rytidosperma vestitum (Pilg.) Connor & Edgar	SE Asia	New Guinea, Papua New Guinea, widespread	Politically inaccessible		DNA extraction	RBG Kew DNA bank
Rytidosperma oreoboloides (F.Muell.) H.P.Linder	SE Asia	Sumatra, Sabah, Philippines, Celebes, New Guinea	Politically inaccessible		DNA extraction	RBG Kew DNA bank
Schismus arabicus Nees	(AU)	Introduced from N. Africa to W.A. and S.A.	Time limitations prevented visiting this area		dried plant material	N. Walsh
C. Taxa of uncertain rank or status						
Austrodanthonia caespitosa var 'swamp'	AU	Glenelg River area, Vic.	Awaiting formal description at species rank		silica	
Austrodanthonia setacea 'big'	AU	Bungalook Conservation Reserves, Vic.	Local morphotype?		silica	
Austrdanthonia pilosa 'dark'	AU	Bungalook Conservation Reserves, Vic.	Local morphotype?		silica	
Austrodanthonia sp. 'Goomalling'	AU	W.A.	Awaiting formal description at species rank		silica	T. Macfarlane
Austrodanthonia setacea var. breviseta	AU	W.A.	Awaiting formal description at species rank		silica	T. Macfarlane
D. Species at 'risk' we were able to collect						
Rytidosperma telmaticum Connor & Molloy	NZ	Canterbury and Otago, South Island		At Risk/Range Restricted[1]		
Austrodanthonia mera (Connor & Edgar) H.P.Linder	NZ	North Island and South Island		Sparse[1]		
Austrodanthonia popinensis (D.I.Morris) H.P.Linder	AU	Tas.		Endangered[3]		
Rytidosperma pumilum (Kirk) Clayton & Renvoize ex Connor & Edgar	AU/NZ	AU: Mt Kosciuszko,N.S.W.; NZ: Volcanic Plateau, North Island; along and to the east of the Main Divide, South Island		Vulnerable[3]		
Rytidosperma nitens (D.I.Morris) H.P.Linder	AU	Tas.		Rare[2]		

[1]New Zealand Threatened Plant Committee
[2]Rare or Threatened Australian Plants
[3]Environment Protection and Biodiversity Conservation Act (Australia)

We obtained material for 82/101 species in the Rytidosperma clade (81%), represented by 115 accessions. Twenty seven species, primarily those that are geographically widespread (e.g. *N. gracilis* or *R. pumilum*) or morphologically variable (e.g. *A. caespitosa*) (Appendix A), are represented by multiple accessions. We also included six taxa of tentative status (possible subspecies or species awaiting description) but other than these we did not attempt to include all described infraspecific taxa. Given that a handful of New Zealand taxa seem to have been driven to extinction by recent damage to native grassland (H. Connor, pers. comm.), and that we did not sample in New Guinea, we were able to include a fair representation of 'available' species diversity (Table 2). Outgroup taxa (*Cortaderia fulvida* (Buchan.) Zotov, *Danthonia alpina* Vest, *Lamprothyrsus peruvianus* Hitchc., and *Pseudopentameris macrantha* (Schrad.) Conert) were chosen to represent the most closely related clades found in the analyses of Pirie et al. (2008). Plant material was collected in the field during the austral summer of 2005–2006 and dried in silica gel. Voucher specimens are housed at Z or BOL if not otherwise indicated (Appendix A).

Table 2. Number of unsampled species per genus.

Genus	Unsampled	Total
Austrodanthonia	3	28
Joycea	0	3
Notodanthonia	1	5
Rytidosperma	11	38
Schismus	1	5
Karroochloa	0	4
Tribolium	0	10
"Merxmuellera"	1	5
"Danthonia"	2	3
TOTAL	**19**	**101**

Molecular marker selection

We filled in the gaps in the datasets used by Verboom et al. (2006) and Pirie et al. (2008) for the non-coding regions *atpB-rbcL*, the *rpl16* intron, *trnL-trnF* and protein coding regions *ndhF*, *matK* and *rbcL* of chloroplast DNA (cpDNA) and *ITS* of nuclear ribosomal DNA (nrDNA) (Appendix A). With the aim to improve resolution within the Rytidosperma clade we sampled two further non-coding cpDNA regions: *trnT-trnL*, which has been shown to be useful at the species level in the Danthonioideae (Galley and Linder, 2007) and *trnD-psbM-ycf6-trnC*, which has been recommended for use at the species level based on trials on diverse plant groups (Shaw et al., 2005) (Appendix A). More conservative coding regions (*matK*, *rbcL*) were sequenced for a selection of placeholder taxa only, following the sampling strategy of Pirie et al. (2008). Primer use largely followed Pirie et al. (2008), with deviations indicated in Table 3.

DNA extraction, amplification and sequencing

Total DNA was extracted using the DNeasy Plant Mini Kit (Quiagen GmbH, Germany), deviating only from manufacturer's protocol in using 3 µl RNase instead of 4 µl and increasing the incubation time with RNase from 10 to 30 min. Attempts to extract useful DNA from herbarium material using both a modified version of the CTAB method (Smith et al., 1991) and the DNeasy Plant Mini Kit failed. In some

cases DNA was obtained, but the quality was not sufficient to amplify regions of interest.

Polymerase Chain Reactions (PCR) were performed in Biometra thermocyclers (T-1 thermoblock, Göttingen, Germany) or Techne (TC-412, Cambridge, UK) in reaction volumes of 25 µl of 2.5 µl PCR buffer (10x, Sigma), 2.5 µl $MgCl_2$ (25 mM) (Sigma, Germany), 4.0 µl dNTPs (1.25 mM) (New England Biolabs or Promega), 0.8 µl each of the two primers (10 µM) (Microsynth AG, Switzerland), 0.15 µl Taq DNA polymerase (5 U/µl) (Sigma, Germany) and 1 µl DNA template, with the final volume made up with ddH_2O. To increase yields for marker regions and/or DNA templates that were otherwise difficult to work with 1.0 µl BSA (5 µg/µl) and in some cases 1.0 µl DMSO (5%) were added. PCR cycling programmes were as follows: an initial 4 min at 94 °C followed by 30–35 cycles of 30 s at 94 °C, 1 min at 50–55 °C, 1–3 min at 72 °C (time and temperature depending on the length of the product and on previously identified specificity of amplification at lower temperatures), terminated by a final extension period of 5 min at 72 °C. Purification of PCR products was done using GenElute PCR Clean-Up Kit (Sigma, Missouri, USA) with a final elution volume of 30 µl or with GFX PCR DNA Purification Kit (Amersham Biosciences, Buckinghamshire, UK), using only 250 µl of capture and wash buffers and 30 µl of elution buffer. Amplification and purification results were visualised on 1.5% agarose gel, stained with ethidium bromide. Cycle sequencing was carried out in a reaction mix of 1.0 µl BigDye Terminator (version 3.1, Foster City, CA, USA), 1.0 µl buffer, 0.5 µl primer, 5.5 µl ddH2O and 0.5–3.0 µl purified PCR product in a 3130xl Genetic Analyzer (Applied Biosystems).

Table 3. Primers used in this study. Those marked in bold indicate deviation from those used by Pirie et al. (2008).

Region	Primer	Use	Sequence/Reference
trnL-F	TabC, TabF	PCR + sequencing	(Taberlet et al., 1991)
rpl16 intron	F71, R1000	PCR + sequencing	(Baum et al., 1998; Galley and Linder, 2007, resp.)
ITS	L, 4	PCR + sequencing	(Baum et al., 1998)
rbcL	Z1, R3; F2, 1374R	PCR + sequencing	(Barker et al., 2007)
matK	Mk_F1 or s51F*, mk_R1*	PCR	(*Hilu et al., 1999; Moline and Linder, 2005)
	s51F*, W*, 1210R*, 7B*, 9R*, mk_R1	sequencing	(*Hilu et al., 1999; Moline and Linder, 2005)
*atp*B-*rbc*L	f1c, r1a2	PCR + sequencing	(Hardy and Linder, 2005)
	atpBrbcL_intF, atpBrbcL_intR	PCR + sequencing	(Galley and Linder, 2007)
ndhF	1F, **1318R,** 972F, 2110R	PCR + sequencing	(Olmstead and Sweere, 1994)
trnT-L	**TabA**	PCR + sequencing	(Taberlet et al., 1991)
	TabB	PCR + sequencing	(Taberlet et al., 1991)
	Danth_trnTL_intF	PCR + sequencing	This study: 5'-GGA AAB CCS TAA AAC G-3'
	Danth_trnTL_intR1	PCR + sequencing	This study: 5'-GTA TTA GAT TAT TCG TCY GAK CC-3'
	Ryt_trnTL_intR1	PCR + sequencing	This study: 5'-GTA TTA GAT TAT TCG TCC GAG CC-3'
trnC-D	**trnDR**	PCR + sequencing	(Shaw et al., 2005)
	psbMR	PCR + sequencing	(Shaw et al., 2005)
	psbMF	PCR + sequencing	(Shaw et al., 2005)
	yof6R	sequencing	(Shaw et al., 2005)
	yof6F	sequencing	(Shaw et al., 2005)
	trnCF	PCR + sequencing	(Shaw et al., 2005)

Sequence alignment, indel coding, matrix combination and identification of 'walking taxa'

Sequences were assembled and edited in Sequencher 4.6 (Gene Codes Corporation; MI, USA) and aligned manually in MacClade 4.07 (Maddison and Maddison, 2005). Manual alignment was deemed appropriate since alignment was unambiguous for all regions of all markers, except for the particularly length variable *trnT-trnL* and *atpB-rbcL* spacers, from which a ca. 20 base pair (bp) poly-T region was excluded. Cloning of the nuclear-encoded *ITS* locus was not carried out, since no multiple peaks were detected in the sequence chromatograms. Indel characters were coded in SeqState 1.25 (Müller, 2005a) using the simple indel coding option of Simmons and Ochoterena (2000). Coded indel characters were checked manually to ensure all missing and ambiguous data had been treated appropriately.

Each marker was first analysed separately to assess behaviour of individual sequences and to inspect for evidence of incompatibility among markers. Explorative parsimony analysis was carried out in PAUP* 4.0b10 (Swofford, 2000): 5000 replicates of heuristic search, random addition sequence (RAS), holding one tree per sequence. Branch swapping was done by tree-bisection-reconnection (TBR), saving no more than 10 trees in each replicate. Given that the chloroplast markers are part of a single, non-recombining, genomic unit conflict between individual gene trees would only be expected in cases of experimental error. Manual inspection of trees resulting from analysis of individual chloroplast markers revealed no such evidence (BS 70%). All chloroplast regions were therefore combined in a single matrix. No further formal test of incongruence was carried out because the best understood of such tests, the incongruence length difference test (ILD; Mickevitch and Farris, 1981) and the Templeton test (Templeton, 1983) have repeatedly been shown to be unreliable (e.g. Sullivan, 1996; Cunningham, 1997; Ramirez, 2006). Resolution in the strict consensus resulting from analysis of the ITS dataset was very limited and bootstrap analysis (1000 replicates with heuristic searches, 10 RAS, with TBR on each round of bootstrap analysis) revealed only 20 nodes with BS $\geq$ 70% (see electronic Appendix I). Five of these 20 nodes are in conflict with nodes with BS $\geq$ 70% in the combined cpDNA tree. One of the conflicting nodes is deep in the tree and depicts 90% of the taxa, one is intermediate and depicts 6% of the taxa and the other three are tip nodes, each depicting only two taxa. As the ITS tree was too poorly resolved to be useful in its own right or to identify (and appropriately treat) possible further conflict prior to combination no further analyses were carried out on the ITS dataset.

To assess the positional stability of individual accessions in the combined cpDNA phylogeny we used the Taxon Instability Among Trees function in Mesquite 2.6 (Maddison and Maddison, 2009) using all most parsimonious trees resulting from explorative analyses as input. Taxa that are placed differently in different trees have a high overall patristic distance and are identified as unstable 'walking taxa'. To test whether such instability might be the result of missing data ("?") we plotted the 'taxon instability' against the amount of missing data for each accession as implemented in Mesquite.

Parsimony analyses and monophyly testing

All characters were treated as unordered (Fitch parsimony, Fitch, 1971) and of equal weight. Indels were coded as missing "–", missing data as unknown "?" and uncertainties following the IUPAC code. Initial searches resulted in hundreds of very similar trees and poorly resolved consensus trees. To enable more tree space ('tree islands') to be searched we used the parsimony ratchet described by Nixon (1999). We carried out two independent runs of 200 ratchet iterations as implemented in PAUP* using Pauprat (Sikes and Lewis, 2001), from which all shortest, unique trees were used as starting trees for a second round of heuristic searches with TBR branch

swapping, saving only one tree per replicate, until 10,000 shortest trees were found. Strict consensus trees of both the pools of shortest trees were calculated and inspected manually as a measure of having adequately explored tree space. If the strict consensus trees are identical, it is assumed that they are an adequate representation of the strict consensus of all shortest trees, even if not all the shortest trees have been found.

Several recently published phylogenies (e.g. Draper et al., 2007; Grimm et al., 2007; Grimm and Denk, 2008; Kocyan et al., 2008) present bootstrap support values calculated following the findings of Müller (2005b), that increased search effort beyond the use of one simple addition search with TBR branch swapping do not affect bootstrap support values. However, none of these studies test whether this holds true for their dataset although it is known that the outcome of bootstrap analyses may be highly dataset dependent (DeBry and Olmstead, 2000, Mort et al., 2000; Sanderson and Wojciechowski, 2000). Further, Müller's (2005b) conclusions have been extrapolated for use under RAS too (Renner et al., 2007; Komarova et al., 2008). To test the possible influence of RAS versus simple addition sequence and few versus many bootstrap iterations on the present dataset we ran four separate bootstrap analyses with full heuristic searches, holding one tree per taxon addition sequence, with TBR branch swapping: (1) RAS-500:500 bootstrap replicates, each of 50 replicates of RAS, saving no more than 10 trees in each replicate; (2) RAS-10,000:10,000 bootstrap replicates, each of 1 replicate of RAS, saving no more than one tree per replicate; (3) SIMPLE-500:500 bootstrap replicates, simple addition sequence, holding up to 50 trees during TBR branch swapping; (4) SIMPLE-10,000:10,000 bootstrap replicates, simple addition sequence, holding up to 50 trees during TBR branch swapping. Differences between support values retrieved from the respective analyses were evaluated statistically using Wilcoxon's signed rank test, a sign test and a correlation analysis.

Parametric bootstrapping (Hillis et al., 1996; Huelsenbeck et al., 1996) was carried out to test whether constraining each of the four genera (Linder and Verboom, 1996) as monophyletic causes a difference in tree length that is significantly different from a length difference that can be attributed to stochasticity in the process of molecular evolution. Heuristic searches (200 replicates of RAS, holding 10 trees per step and with TBR branch swapping, keeping 10 trees of score 1) were carried out on the original dataset in PAUP* with and without each of the four genera *Austrodanthonia*, *Joycea*, *Notodanthonia* and *Rytidosperma* constrained to be monophyletic. Based on the most appropriate model of nucleotide sequence evolution, as estimated in Modeltest 3.7 (Posada and Crandall, 1998) using only DNA characters, 100 new datasets were simulated in SeqGen (Rambaut and Grassly, 1997) and constrained and unconstrained analyses were carried out on each of the new matrices as above. The resulting length differences ($constrained_{sim}$–$unconstrained_{sim}$) were plotted as a frequency diagram and used as a null distribution of length differences, against which the length difference ($constrained_{obs}$–$unconstrained_{obs}$) was assessed.

Bayesian analyses

The most appropriate model of nucleotide evolution was determined in Modeltest3.7 (Posada and Crandall, 1998) for each of the cpDNA markers separately, using the Akaike Information Criterion (AIC) (Akaike, 1973), which allows quantification of model selection uncertainty (Posada, 2003; Posada and Buckey, 2004). For most regions the General Time Reversible (GTR) model was found to be the best or well supported, but for three datasets the Transitional model (TIM) model had a lower AIC value. Loss of information caused by using the GTR model in these three cases is shown in Table 4. Since Bayesian analysis is relatively robust to slight over-parameterisation (Ronquist et al., 2005), we analysed all cpDNA regions using the

same model of nucleotide sequence evolution (GTR+I+G) as implemented in MrBayes v3.1.2 (Ronquist and Huelsenbeck, 2003). The data were separated into three partitions: coding regions (*matK*, *rbcL*, *ndhF*), non-coding regions (*trnL-F*, *trnT-L*, *rpl16* intron, *atpB-rbcL*, *trnC-D*) and indels ('gap' characters). Indels were analysed using a F81-like binary model, assuming equal rates of shifts between (0) and (1) and no all-absence or all-presence characters. Markov Chain Monte Carlo (MCMC) analysis was carried out, sampling every 10^3 generations, in four independent runs, each with four simultaneous MCMC chains. The sampled parameter values and trees were checked using Tracer v1.4 (Rambaut and Drummond, 2007) and AWTY (Wilgenbusch et al., 2004; Nylander et al., 2008), respectively, to ensure convergence and sufficient sampling of the four runs and to identify the number of burnin generations. After 20 x 10^6 generations the effective sample size (ESS) for all parameters and for all runs was >100 and clade posterior probabilities were consistent between runs and generations. However, three of the runs converged at a mean log likelihood (LnL) of -43420, while the fourth run reached a better likelihood plateau (LnL = -42740). Given the failure of independent runs to converge at the optimal likelihood we started a second analysis of four independent runs, providing the tree with the highest posterior probability from the optimal run in the first analysis as a starting tree. In each of the runs the starting tree was perturbed 10 times (nperts = 10) and in two of the runs the number of chains was increased to eight. Two of the runs converged at LnL = -43420 after five or 10 x 10^6 generations (eight or four chains, respectively) and a third after 14 x 10^6 generations. All runs were left to run until they had reached 31 or 65 x 10^6 generations, depending on the number of chains, but the fourth chain never reached the same likelihood plateau (LnL = -43750) and none of the runs reached as optimal a likelihood plateau as that found in the first analysis. Post burnin trees from suboptimal and optimal runs were summarised as 50% majority rule consensus trees in various combinations (see Section 2). The percentage of trees in which each node is present corresponds to its posterior probability (p.p.).

Table 4. Selection of model of molecular evolution using the Akaike Information Criterion (AIC).

Marker	Best fit model	Model chosen	Δ AIC	Δ $AIC_{GTR+I+G}$
atpB-rbcL	GTR + I + G	GTR + I + G	-	-
ndhF	TVM + I + G	GTR + I + G	1-2	-
rbcL	K81uf + I + G	TIM + I + G	1-2	5.53
rpl16 intron	K81uf + I + G	TIM + I + G	1-2	2.99
matK	TVM + G	GTR + I + G	1-2	-
trnC-D	TVM + I + G	GTR + I + G	1-2	-
trnL-F	TIM + I + G	TIM + I + G	-	3.21
trnT-L	GTR + I + G	GTR + I + G	-	-

Morphological data and cladistic analyses

We compiled 249 characters (225 synapomorphic parsimony informative) for 94 ingroup taxa, plus three outgroups (*Pseudopentameris macrantha*, *Cortaderia fulvida*, *Lamprothyrsus peruvianus*). These were scored from our DELTA (Dallwitz, 1980) database (HPL) and personal observations (AMH). Forty five continuous characters were coded as two or three states in such a way that the number of polymorphic taxa was minimised. Characters and character states are listed in Appendix B.

Morphological characters were analysed in PAUP* using two independent runs of 200 parsimony ratchet iterations (Nixon, 1999) as outlined above. All characters were equally weighted (EW) and unordered (Fitch parsimony, Fitch, 1971), gaps or inapplicables were coded as missing "–" and uncertainties as unknown "?". Since most parsimonious trees (MPTs) found in both runs were of the same score

and their strict consensus trees were identical, we did not swap further on those trees. Instead, they were all pooled and used as a starting point for successive weighting (SW) analysis (Farris, 1969) in which the contribution of each character was weighted according to its rescaled consistency index, RC (Farris, 1989). Successive weighting was carried out in a two-stage analysis (Willmott and Freitas, 2006) in which 2000 replicates of TBR branch swapping were carried out and the most parsimonious trees found used as a starting point for a second round of TBR branch swapping which was continued until 10,000 trees were found. These two stages were repeated until character weights stabilised and identical trees were found.

Branch support was calculated on the SW matrix in PAUP with 1000 replicates of bootstrap analysis with full heuristic search, simple sequence addition, holding 10 trees per step, TBR branch swapping, saving no more than 5 trees each replicate. The validity of a bootstrap analysis on the morphological dataset is debatable, since there are probably not enough characters to carry out a reliable test (Zander, 2003), and since it assumes independence of characters. Therefore, also Bremer support (Bremer, 1994) was calculated using AutoDecay 5.0 (Eriksson, 2001) in conjunction with PAUP*. One topological constraint was defined for each branch present in one of the MPTs from the successive weighting analysis and heuristic searches (100 replicates of RAS with TBR, holding 10 trees each step) were run for each constraint using the 'reverse constraints' method. The decay index represents the increase in tree length required to satisfy the constraint (=collapse of a given branch). Finally, unambiguous character state changes were mapped on to one of the MPTs using the Trace All Changes command in MacClade.

Comparison of plastid tree with morphology, ecology and distribution

Morphology

First the topologies from the respective analyses were examined for node to node congruence. Then, the difference between the mean RC for each morphological character across the morphological cladogram and the respective mean RC across the 100 Bayesian trees with the highest posterior probability was evaluated using Wilcoxon's signed rank test (n = 225). Finally, we ranked the characters according to their maximum RC across both sets of trees to see which characters fit the respective topology the best. The distribution of character states of best fitting characters across each topology (number of steps) was compared to that expected by chance, by generating 1000 random topologies in Mesquite (either using the Random Branch Moves or Reshuffle Terminal Taxa commands).

Ecology and distribution

Ecology and distribution characters were scored from descriptions and floras (Veldkamp, 1993; Curtis and Morris, 1994; Jacobs, 1993; Walsh and Entwistle, 1994; Baeza, 1996, 2002; Edgar and Connor, 2000; Darbyshire, 2003; Linder, 2004; Veldkamp, 2004, unpublished notes; Molloy and Connor, 2005; Marsden, 2006), personal observations (AMH) and DELTA (HPL) (Table 5). All characters were optimised over the 1000 Bayesian trees with the highest posterior probability using parsimony as implemented in Mesquite. Number of steps required for each character on the observed topology was compared to a null distribution of parsimony character steps generated by performing 1000 Random Branch Moves on one of the trees, 1000 times. Character 6, collection locality, was coded as the state in Australia or New Zealand or country in Africa from which each specimen was collected, regardless of the range occupied by the species. This was done to be able to trace the geographical component in cpDNA signal.

Table 5. Ecology and distribution characters (optimised onto plastid tree).

Character	States	Parsimony steps (obs)	Parsimony steps (random)	P value
Altitude	(0) < 650m (1) to 2150m (2) > 2200m	66–69	69–85	< 0.01
Habitat	(0) grassland in full sun (1) lightly shaded woodland (2) shaded riverine forest (3) sclerophyll shrubland (4) rock ledges (5) renosterveld (6) Namaqua broken veld (7) sand dunes (8) peat bogs (9) arid shrubland/grassland (10) damp ground/wet grassland (11) feldmark	73–74	81–86	< 0.01
Parent rock type	(0) limestone (1) sandstones (2) basalts (3) granite (4) shales (5) laterite (6) serpentinite	112–113	119–133	< 0.01
Moisture regime	(0) well drained soils (1) seepages and wetter habitats (2) marshes and bogs (3) stream banks	50–51	55–62	< 0.01
Continental distribution	(0) Africa (1) Australia (2) New Zealand (3) South America (4) Europe (5) Asia (6) East Indies	21–22	48–61	< 0.01
Collection locality	(0) WA (1) VIC (2) ACT/NSW (3) TAS (4) SA (5) Marlborough (6) Otago (7) CH (8) Asia (9) S. Africa (10) Namibia (11) North Island (12) Canterbury (13) Chile (14) Indo	43–46	68–85	< 0.01

Table 6. Behaviour of individual molecular markers under parsimony; number of taxa, number of sequences, aligned sequence length, parsimony informative (PI) bases, parsimony informative (PI) insertion-deletion characters (indels), total informative characters (Tot. inf. c), characters per taxon (C/Tax), characters per sequence (C/Seq), tree length, consistency index (CI) and retention index (RI).

	No. taxa (no. of seq's)	Aligned seq. length	PI bases	PI indels	Tot. inf. c	C/Tax	C/Seq	Tree length	CI	RI
trnL-F	88 (122)	1012	93	30	123	1.40	1.01	351	0.712	0.815
rpl16 intron	89 (120)	1055	101	45	146	1.64	1.22	453	0.748	0.840
atpB-rbcL	91 (122)	1002	73	26	99	1.09	0.811	333	0.664	0.806
trnT-L	87 (118)	768	84	30	114	1.31	0.966	359	0.713	0.811
trnD-C	79 (107)	3051	222	92	314	3.40	2.93	937	0.763	0.825
rbcL	49 (52)	1338	49	0	49	1.00	0.942	135	0.733	0.836
ndhF	88 (118)	2043	189	14	203	2.31	1.72	683	0.694	0.795
matK	45 (49)	1917	169	13	182	4.00	3.71	1643	0.875	0.656
ITS	77 (97)	640	148	22	170	2.20	1.75	648	0.551	0.753
Comb. cpDNA	88 (119)	12712	911	245	1156	13.1	9.70	3996	0.691	0.766

Results

3.1. Behaviour of individual marker regions and accessions

Numbers of parsimony informative DNA and indel characters for the individual matrices are shown in Table 6, along with tree statistics of explorative parsimony analyses on each partition separately. Two accessions of *A. penicillata* (Labill.) H.P. Linder and the single accession of *R. vestitum* (Pilg.) Connor and Edgar were found to be relatively unstable in the Taxon Instability Among Trees analysis of the combined cpDNA dataset (results not shown). These were therefore removed. Three more taxa were removed upon manual inspection of the most parsimonious trees (one of the accessions of A. racemosa (R.Br.) H.P. Linder, *A.* sp. 'Goomalling' (A.G. Gunness et al. OAKP 10/63) and *R. fortunae-hibernae* (Renvoize) Connor and Edgar). These taxa were not identified as particularly unstable in the above test because their positions were consistent across most of the trees, hence their overall low patristic distance. In

a few trees, however, their positions were markedly different and this had a disproportionally high impact on the resolution of the strict consensus. No relationship between the amount of missing data and the patristic distance across the trees was found ($R^2 = 0.0108$, results not shown), indicating that the degree to which taxa 'walk' is not directly related to the proportion of missing data and is therefore not an artefact of the sampling strategy adopted. Six taxa represent 5% of the taxa in the current dataset, which is equivalent to the outer percentiles often removed from a dataset to leave the 95% credibility set. Upon removal of these taxa a much more resolved and robust topology was achieved. The final matrix of 115 accessions (representing 80 species, five tentative taxa, plus four outgroups) and 12,712 aligned characters forms the basis for the remainder of this paper.

Table 7. Bootstrap analyses, comparison of support values and running time. A. Comparison of all nodes. B. Comparisons where BS ≥ 80% for nodes in at least one of the analyses. C. Comparisons where BS = 50-70%.

A. All nodes.

Comparison[1]	# nodes equal	# nodes higher (%) (*analysis time*)	# nodes lower (%) (*analysis time*)	P (Wilcoxon's signed rank test)	P (Sign test)	r^2
RAS-500: RAS-10,000	38	+40 (1-5) (*14 h*)	-14 (1-4) (*1 h*)	< 0.01	< 0.01	0.991
SIMPLE-500: SIMPLE-10,000	42	+31 (1-5) (*4 h*)	-23 (1-4) (*78 h*)	*n.s.*	*n.s.*	0.993
RAS-500: SIMPLE-500	23	+36 (1-31)	-39 (1-14)	*n.s.*	*n.s.*	0.900
RAS-10,000: SIMPLE-10,000	45	+35 (1-31)	-16 (1-10)	< 0.01	0.01	0.915

B. Nodes BS=80–100%.

Comparison[1]	# nodes equal	# nodes higher (%)	# nodes lower (%)	P (Wilcoxon's signed rank test)	P (Sign test)	r^2
RAS-500: RAS-10,000	32	+6 (1-3)	-9 (1-5)	*n.s.*	*n.s.*	0.953
SIMPLE-500: SIMPLE-10,000	30	+15 (1-4)	-6 (1)	*n.s.*	*n.s.*	0.968
RAS-500: SIMPLE-500	19	+22 (1-31)	-11 (1-7)	0.04	*n.s.*	0.759
RAS-10,000: SIMPLE-10,000	32	+14 (1-31)	-6 (1-5)	0.04	*n.s.*	0.760

C. Nodes BS=50–79%

Comparison[1]	# nodes equal	# nodes higher (%)	# nodes lower (%)	P (Wilcoxon's signed rank test)	P (Sign test)	r^2
RAS-500: RAS-10,000	4	+27 (1-5)	-7 (1-4)	< 0.01	< 0.01	0.942
SIMPLE-500: SIMPLE-10,000	11	+16 (1-5)	-17 (1-3)	*n.s.*	*n.s.*	0.951
RAS-500: SIMPLE-500	4	+26 (1-14)	-19 (1-31)	*n.s.*	*n.s.*	0.480
RAS-10,000: SIMPLE-10,000	13	+11 (1-12)	-26 (1-31)	0.02	0.02	0.567

[1]Analyses. RAS-500: 500 bootstrap replicates, heuristic search with 50 RAS's on each; RAS-10,000: 10,000 bootstrap replicates, heuristics search with 1 RAS on each; SIMPLE-500: 500 bootstrap replicates, heuristic search with simple taxon addition; SIMPLE-10,000: 10,000 bootstrap replicates, heuristic search with simple taxon addition. Branch swapping was by the TBR algorithm throughout.

Plastid tree as inferred from parsimony analyses

The first round of the parsimony ratchet resulted in 36 trees of 3996 steps (CI = 0.691; RI = 0.766; Table 6) and the repeat analysis resulted in 30 trees of the same tree scores. The second rounds of swapping resulted in two identical strict consensus trees (not shown).

Bootstrap analyses took between one and 78 h to complete and revealed four different sets of node support values. Under simple addition sequence, differences in the number of bootstrap replicates did not lead to significantly different results (Table 7A–C, $r^2 \geq 0.95$ for all comparisons), suggesting that for a medium sized dataset analysed under simple taxon addition increasing the number of bootstrap replicates does not significantly alter BS support values. In contrast, under RAS, differences in number of bootstrap replicates and search strategy had a significant effect on support values of less well supported nodes even though support values were highly correlated (Table 7A–C, $r^2 \geq 0.94$ for all comparisons). Müller's (2005b) findings ought thus not be interpreted as applying to RAS. Simple addition sequence versus RAS resulted in marginally significant differences for well supported nodes (80%) (Table 7B, $r^2 = 0.76$) and significant differences for less well supported nodes when more bootstrap iterations were run but not when fewer bootstrap replicates were run (Table 7C). However, support values from these two analyses were the least correlated of all comparisons ($r^2 = 0.57, 0.48$), indicating that differences are greater and more scattered, even if they are symmetrical. Overall, the proportion of nodes that was unaffected was much higher for nodes with a BS 80–100% than for nodes with a BS of 79% or below but influence of search strategy on more robust nodes warrants caution as these nodes often form the basis of evolutionary or taxonomic inferences. In Fig. 1 bootstrap values from analysis SIMPLE-10,000 are displayed.

Parametric bootstrapping resulted in a null distribution of length differences ($constrained_{sim}$–$unconstrained_{sim}$) ranging between 0 and 7 steps. The observed length difference ($constrained_{obs}$–$unconstrained_{obs}$) was 164 steps, which is significantly higher ($P < 0.01$), meaning that the null hypothesis of length differences being due to stochasticity is rejected.

Plastid tree as inferred from Bayesian analyses

In the first analysis mean LnL was significantly higher for run 1 (-42740) than for the other three runs (-43420) ($P < 0.001$, t-test, df = 44998). Posterior split probabilities were constant across samples and among runs, after a burnin of 10–25% was removed. Upon calculation of a 50% majority rule consensus tree for each of the runs separately, representing 8000 (runs 1 and 4) or 5000 (runs 2 and 3) optimal trees, three topological differences were apparent: the positions of *A. fulva* and (*R. setifolium, R. cf. corinum, R. petrosum*) were different in run 1 (p.p. = 0.60, 0.98, respectively) compared to the other three (p.p. = 0.99–1.0 for both nodes) and the position of *A. diemenica* differed in run 4 (p.p. = 0.97), compared to the other three (p.p. = 0.80–0.86).

In the second analysis the three best runs converged at the less optimal likelihood plateau of the previous analysis (-43420). A consensus tree of the 87,239 trees (total ESS = 541) remaining after 1/3 of the trees from each run had been removed as burnin, revealed the same topology as the previous consensus tree with the same mean likelihood, except the position of *A. diemenica* which was no longer different from that in run 1 in the previous analysis. Since we are able to demonstrate that only minor topological differences underlie the statistical differences we have chosen to use the 8000 trees from the single run with the best likelihood score as our phylogenetic hypothesis (Fig. 1). This is more resolved than the results from the parsimony ratchet analysis and congruent in all but four nodes, none of which is well

supported in the parsimony analysis (BS = 51–64%), thus they are not considered to represent conflict (not shown).

The most early diverging clade consists of six tough, wiry grasses from Africa and the Himalayas that are members of the poly- or paraphyletic genera *Danthonia* and *Merxmuellera* (clade A, BS = 73%, p.p. = 0.99, Fig. 1). *Schismus* plus *K. schismoides* are sister to the remainder of the species (clade B, BS = 98%, p.p. = 1.0) and *Karroochloa* and *Tribolium* form a well supported clade (clade C, BS = 100%, p.p. = 1.0) sister to all the species from Australia, New Zealand, South America and New Guinea (clade D, BS = 100%, p.p. = 1.0). It is notable that despite the amount of data included, branch lengths are remarkably short in clade D compared to clades A, B and C.

Within clade D, there are three major clades: clades E (BS = 100%, p.p. = 1.0), F (BS = 55%, p.p. = 0.98) and G (BS = 52%, p.p. = 0.94). The relationship among these clades is not resolved. Clade E consists of four small, primarily montane species from New Zealand and one species with a disjunct distribution between New Zealand and the Snowy Mountains in Australia (*R. pumilum*). Clade F consists of two robust clades: H and I. Clade H (BS = 76%, p.p. = 1.0) comprises all the Andean taxa (clade Hi, BS = 99%, p.p. = 1.0) and a clade (Hii, BS = 70%, p.p. = 1.0) of both lowland and highland species from New Zealand, two of which (*N. gracilis and R. australe*) are also native to the Australian highlands. Clade I (BS = 70%, p.p. = 1.0) comprises three clades representing morphological extremes: large species with very hairy lemma backs in two unsupported clades, Ii and Iii, that are not well supported (BS < 50%, p.p. = 0.60; 0.61, respectively) and one clade of all the species with glabrous or much reduced indumentum on the lemma backs (clade Iiii, BS = 70%, p.p. = 1.0). All the species in Clade G are Australian and most of the species are widespread in the lowlands of SE Australia. There is less internal support within this clade and subclades are not always easy to characterise. Of note is a clade of three species that prefer wet environments (clade Gi, BS = 100%, p.p. = 1.0) and a clade uniting the species with broad lemmas (Gii, BS = 99%, p.p. = 1.0). Finally, it is noteworthy that the multiple accessions of *A. caespitosa* and *J. pallida* are found in phylogenetically distant positions.

Morphological cladogram

Equally weighted ratchet analyses yielded 256 MPTs of 2548 steps (CI = 0.179; RI = 0.456) in the first run and 134 MPTs of identical score in the second run. Their respective strict consensus trees are identical. The successive weighting analysis resulted in a stabilised topology after the third iteration, but tree length varied between iterations two and three (L = 181.588 to L = 184.450), suggesting the presence of more than one weighting scenario underlying the optimal topology. We thus carried out two more iterations, after which tree length continued to vary slightly (from L = 181.624 to L = 181.886), but the optimal topology remained unchanged and the overall CI stabilised at 0.253 and the RI at 0.559. The single most parsimonious tree found in the last iteration is presented in Fig. 2.

In this, species are essentially arranged into a grade, terminating in two sister clades, L and Q (Fig. 2). Trends largely corresponding to the seven genera can be identified: species of Austrodanthonia form the 'basal' grade, bar the large, wiry African '*Merxmuellera*' species; *Rytidosperma* largely corresponds to clade R; *Karroochloa* to clade M; *Schismus* to clade N; and *Tribolium* to clade O. All but one species of *Notodanthonia* are found in clade P and two of the three species in *Joycea* constitute clade J. Nineteen nodes have support BS ≥ 50% of which eight are 70% (Fig. 2). Almost all supported nodes are tip nodes and 12 are within *Karroochloa*, *Schismus* and *Tribolium* (clades M, N, and O). This pattern differs from the strict consensus cladogram resulting from the EW analysis (see electronic Appendix II) only with respect to the position of *Rytidosperma virescens* var. *virescens* and

Figure 1. Bayesian majority rule consensus tree with BS indicated above the branches and Bayesian p.p. values indicated below branches. Nodes with BS < 50%, or which are not present in the strict consensus are indicated by (–). Nodes congruent with morphological topology are marked by a black filled circle (●). Nodes annotated A–I refer to those mentioned in the text. Taxa for which multiple accessions have highly disparate positions are underlined.

Austrodanthonia occidentale and with respect to the level of resolution within clade Q (Fig. 2). Clade P (Fig. 2) is not depicted in the EW analysis, nor is the sister relationships between *Rytidosperma fortunae-hibernae* and *R. pauciflorum* and between *R. mamberanense* and *R. vestitum* and the two terminal clades within clade R (Fig. 2) are only depicted in part. Downweighting the characters that are less consistent with the set of cladograms from the EW analysis thus yielded a more informative cladogram. We therefore use only the single cladogram resulting from the SW analysis for further analyses and discussion.

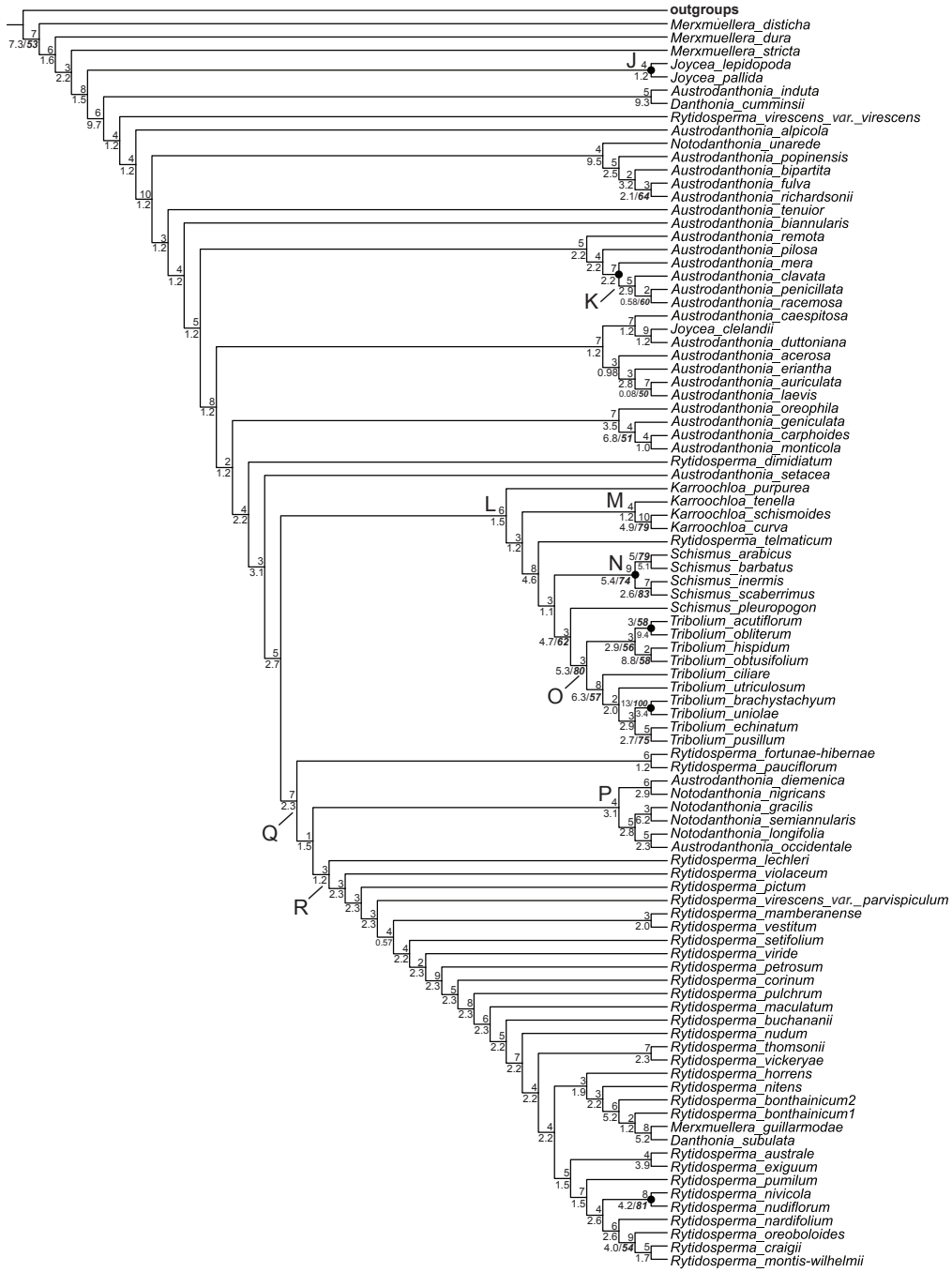

Figure 2. Morphological cladogram. Nodes congruent with the cpDNA tree are marked by a black filled circle (●). Bremer (regular) and BS (*italicised*) support values are indicated below the branches and the number of unambiguous character state changes above the branches.

Match of plastid tree to morphology, ecology and distribution

Morphology
Six congruent nodes were found between the cpDNA tree and the morphological cladogram (Figs. 1 and 2): (1) *A. mera* + *A. racemosa* + *A. clavata* + *A. penicillata* (clade K morphology, clade Iiii cpDNA) if the position of one of the accessions of *A. caespitosa* (AMH25) in the cpDNA tree is disregarded; (2) *R. nivicolum* + *R. nudiflorum*; (3) *J. lepidopoda* + *J. pallida*; (4) Clade M (morphology), in clade B (cpDNA); (5) *T. acutiflorum* + *T. obliterum*; (6) *T. brachystachyum* + *T. uniolae*. None of the congruent nodes falls within clade G of the cpDNA phylogram (Fig. 1).
Overal, mean RC values for each morphological character are significantly different on the morphological cladogram compared to on the plastid trees (Wilcoxon's signed rank test, $P = 0.01$). Of the characters whose RC ranks in the top 10% on each respective topology, only two have the highest RC on both the morphological and plastid topologies: completeness of the upper row of lemma indumentum and caryopsis cross-sectional shape (Table 8). Eight of the 22 characters that rank the highest RC on the morphological cladogram have a distribution of character states that is not significantly different from random (Table 8). Fourteen characters are significantly different at the 1% confidence interval. On the plastid topology only one of the morphological characters with the highest RC has a distribution of character states that is no different from one expected by chance (Table 8) and 15 characters are significantly different from random at the 1% confidence level. Method of generation of randomised trees did not affect the results.

Ecology and distribution
Ancestral state reconstruction of each of the four ecological characters, continental distribution and collection locality on the cpDNA topology revealed that the number of steps required on the observed topology was significantly less than on a random topology ($P < 0.01$) for each (Table 5).

Discussion

A chloroplast tree of the Rytidosperma clade

Despite extensive Bayesian analyses no two runs converged at the optimal likelihood score. However, topological differences between the optimal topology and the less optimal topology are restricted to two nodes, both of which are tip nodes. Tip nodes in this study may not represent phylogenetic positions of individual species (see below) and topological differences at that level do not affect the question of generic delimitation addressed here. Consequently, we consider that any further attempts to seek statistical convergence would be futile.

The plastid tree we present is based on an expansion of existing datasets (Verboom et al., 2006; Barker et al., 2007; Pirie et al., 2008) and accordingly displays a pattern consistent with previous studies. Taxon sampling was only slightly improved upon compared to the most extensive study of the extra-African taxa (Pirie et al., 2008) but characters were sampled much more densely, meaning that for the first time we are able to discuss the phylogenetic position of individual clades with more confidence. But how much of the species phylogeny is reflected by the plastid (bifurcating) tree? Considering that interspecific hybridisation is known to occur in this group of danthonioid grasses (Brock and Brown, 1961; Spies et al., 1992; Visser and Spies, 1994a-d; Waters, 2007) evolution is unlikely to have proceeded linearly. Furthermore, the plastid genome behaves like a single gene. Genomic processes that do not track evolutionary history at the organismal level might therefore cause it to yield misleading inferences of species phylogeny (Doolittle, 1999; Zhang and

Table 8. Rescaled consistency index (RC) of morphological characters that rank the top 10% across the morphological and plastid trees, and their position relative to a random distribution of number of steps. Some characters score high on the morphological topology (86, 110, 186, 187, 204, 205) or plastid topology (46, 71, 103, 192) because of a lot of missing data. Others (*) display a conserved pattern on the respective topology.

Topology	Character	No. states	RC	Steps (obs)	Steps (random)	P value
Morphological	110. density of lodicule microhairs	3	1.00	27	26–35	0.01
	205*. tussock diameter at base	2	1.00	10	10	*n.s.*
	241. anther length	2	0.62	10	13–15	<0.01
	86. setae included in or exerted from glumes	3	0.45	26	29–36	<0.01
	170. abaxial epidermal zonation presence	2	0.45	4	4–5	*n.s.*
	79. lemma lobe length relative to lemma body	4	0.44	43	52–66	<0.01
	84. second lemma lobe setae presence	2	0.44	23	24–28	<0.01
	204. number of chromosome complements	5	0.41	31	32–36	<0.01
	232. second lemma number veins in lobes	3	0.36	25	31–43	<0.01
	117. caryopsis cross-sectional shape	6	0.33	19	18–19	*n.s.*
	212. ligule length	3	0.33	44	43–51	0.01
	210. Inflorescence length	3	0.30	25	22–27	*n.s.*
	85. lemma setae length relative to lemma lobe	3	0.27	37	40–49	<0.01
	34. inflorescence shape	5	0.25	22	34–46	<0.01
	45. glume length relative to the cluster of florets	3	0.25	29	42–58	<0.01
	76. second lemma indumentum between rows	2	0.25	18	21–30	<0.01
	174. intercostal short cell presence and distribution in long cells files	6	0.25	28	25–28	*n.s.*
	194. adaxial prickle hairs presence and barbs presence	3	0.25	9	10–12	<0.01
	195. adaxial prickle distribution	3	0.25	3	2–3	*n.s.*
	243*. caryopsis width	2	0.25	2	2	*n.s.*
	72. upper row of lemma indumentum	3	0.24	17	30–39	<0.01
	184. abaxial microhair relationship between length of basal and distal cells	4	0.24	14	12–16	*n.s.*
Molecular	46. glumes length relative to basal lemmas	3	1.00	3	3–4	*n.s.*
	114. fruit a nut or caryopsis	3	1.00	2	3–4	<0.01
	192. adaxial papillae shape	4	0.45	1–2	2–3	<0.01
	74. second lemma lower row of hair	5	0.33	21	25–29	<0.01
	103. distribution of palea indumentum	3	0.33	6	8–10	<0.01
	142. distribution of 3'vbs relative	4	0.33	3	3–4	0.05
	62. second lemma veins anastomosing	2	0.25	2	2–3	0.01
	141. smaller bundles differentiated	2	0.25	2	2–3	0.01
	207. tussock height	2	0.25	47	47–48	0.05
	247. hilum length:tot caryopsis length	2	0.25	2	2–3	0.05
	128. setaceous, filiform, shape	4	0.23	6–7	7–15	<0.01
	190. abaxial costal silica bodies description	10	0.21	21–22	26–29	<0.01
	100*. palea keels indumentum or ornamentation	4	0.20	12	27–38	<0.01
	117. caryopsis cross-sectional shape	6	0.20	25–26	26–27	<0.01
	14. innovation buds <position>	2	0.19	6	12–15	<0.01
	71. density of scattered hairs on lemma back	3	0.19	8–9	8–12	0.05
	101. palea body texture	3	0.17	5	5–6	0.05
	2. plant growth form	7	0.15	33	46–52	<0.01
	72. upper row of lemma indumentum	3	0.15	27	31–36	<0.01
	136. angle and curvature of rib sides	5	0.14	15–16	20–24	<0.01
	118. caryopsis cross-sectional shape	6	0.14	25	26–28	<0.01
	67*. second lemma indumentum distribution	6	0.14	24	37–46	<0.01

Hewitt, 2003; Ballard and Whitlock, 2004; Spinks and Shaffer, 2009). Explicit methods for deducing species phylogenies from gene trees exist (Lerat et al., 2003; Maddison and Knowles, 2006; Liu et al., 2007; Linnen and Farrell, 2008; Edwards, 2009) but these necessarily rest upon data from entire genomes (Lerat et al., 2003), parts of multiple genomes (e.g. Carstens and Knowles, 2007; Liu et al., 2008; Spinks and Shaffer, 2009) or simulations (e.g. Maddison and Knowles, 2006). Even though we do have data from the nuclear genome (ITS), the tree based on these data is poorly resolved to the point of being uninformative. Such low resolution could be the result of fixation of point mutations, i.e. homogenisation of hybrid sequences by the process of concerted evolution (Wendel et al., 1995; Roelofs et al., 1997; Fuertes Aguilar et al., 1999b). For that to apply low levels of variation among individual sequences would be expected but in fact observed ITS sequences are not particularly homogenous (Table 6) and we attribute low resolution to a simple paucity of parsimony informative characters given the number of taxa. In the absence of independent molecular data we test the reliability of the plastid tree against morphological, ecological and distribution data using the philosophy of 'reciprocal illumination' ("reciprocal clarification" of Hennig (1966); illumination loops and research cycles of Kluge (1997); cycles of character and hypothesis testing of Egan (2006)).

Reliability of the plastid tree – fit with morphology, ecology and distribution

Fit with morphology

Only six nodes in the cpDNA tree are congruent with or uncontradicted by the morphological cladogram (Figs. 1 and 2). Three of these are among the African species in clades B and C and three are in clade F. Those in clade F include *R. nivicolum* and *R. nudiflorum*, two small, overall glabrous species that often co-occur and have been considered to be closely related in the past, on the basis of morphology (Vickery, 1956; Walsh and Entwistle, 1994). *Austrodanthonia mera*, *A. clavata*, *A. racemosa* and *A. penicillata* belong to the group of lowland species in which lemma indumentum is absent or reduced and an association among some or all of these species has been noted repeatedly (e.g. Vickery, 1956; Zotov, 1963; Connor, 1991; Linder, 2004). *Joycea pallida* and *J. lepidopoda* make up two of the three species of the genus *Joycea* and their association on molecular grounds is reassuring rather than surprising. Despite a good fit at a few nodes, most parts of the cpDNA tree are incongruent with the morphological cladogram. In addition, the mean RCs (Farris, 1989) of all characters taken together are significantly different on the morphological topology compared to the cpDNA topology and only two characters score a high RC on both topologies (Table 8). Taken together, these results demonstrate that the morphological and plastid topologies are significantly different. Differences between the morphological and cpDNA topologies may reflect high levels of homoplasy in either or both of the datasets, the plastid tree not representing species phylogeny or reconstruction errors. Considering the extensive analyses, reconstruction errors are unlikely, leaving incongruent plastid and species histories or homoplasy as possible explanations.

Two thirds of the best fitting characters have a distribution on the morphological cladogram that significantly more parsimonious than their distribution on a random topology, whereas on the cpDNA topology all but one character has a significantly more parsimonious distribution than on a random topology (Table 8). This suggests that much more of the signal in the morphological data than the cpDNA data cannot be distinguished from a random signal, meaning that the incongruence between the morphological and plastid trees is likely to be the result of homoplasy in the morphological dataset. The fact that only one of the best fitting morphological characters has a random distribution on the plastid tree lends

confidence to the presence of a phylogenetic signal in the plastid tree that is supported by certain morphological characters.

Fit with ecology and distribution

All optimised ecological characters (altitude, habitat, parent rock type and moisture regime) and continental distribution showed a significantly more parsimonious distribution on the cpDNA topology than on a random topology (Table 5). This suggests that our phylogenetic hypothesis is consistent with the existence of an evolutionary history that is, in part, constrained by geographical and ecological factors and can be explained by phylogenetic niche conservatism *sensu* Crisp et al. (2009).

Distribution of the Rytidosperma clade largely mirrors that of the Danthonioideae as a whole, with species occurring on all Southern Hemisphere continents and Africa being optimised as the ancestral area (Linder and Barker, 2000, 2005; Pirie et al., 2009). Most of the diversity of the Rytidosperma clade is found in Australasia and the non-African members of the Rytidosperma clade (clade D) form a monophyletic group, embedded within the paraphyletic African lineages (Fig. 1). These patterns suggest that establishment of the extra-African distribution was initiated by a single dispersal event out of Africa, followed by a major radiation in Australasia. Molecular dating analysis places the occurrence of this dispersal event between ca. 10 and 3.1 Ma (A. Antonelli, unpublished results), suggesting that the Rytidosperma clade shares its biogeographic history with Gnaphalieae (Asteraceae) (Bergh and Linder, 2009) and possibly parts of Schoeneae (Cyperaceae) (Verboom, 2006) and Anthemideae (Asteraceae) (Himmelreich et al., 2008). Disjunct distributions across the Indian Ocean in these groups were established through dispersal from Africa to Australasia during the Miocene as opposed to in the opposite direction, which seems to have been more prevalent during the early Eocene (Bergh and Linder, 2009). The timeframe in which the Rytidosperma clade is likely to have radiated in Australasia supports predictions that several plant lineages in New Zealand underwent rapid diversification following the onset of mountain building ca. 5–2 Ma (Winkworth et al., 2002b, 2005). Consistent with this, ancestral state reconstructions revealed that the ancestor of the non-African species in the Rytidosperma clade was probably 'montane' (Fig. 3A) suggesting a scenario of colonisation of high elevation areas in Australasia with subsequent colonisation of the lowlands.

Distribution of the Rytidosperma clade also displays a trans-Pacific disjunction. Floristic similarities between southern Chile and New Zealand were noted by (Hooker, 1846, 1853) and Darwin (1859) and according to more recent floristic studies at least 40 genera shared between New Zealand and the Southern Andes have disjunctions that were probably established by dispersal across the Pacific (Wardle et al., 2001; Ezcurra et al., 2008). In the present analysis we found that the Andean species (clade Hi) are sister to a clade of species from New Zealand, two of which occur also in Tasmania (clade Hii). These clades are embedded in a larger Australasian clade, suggesting that the trans-Pacific pattern in the Rytidosperma clade has established following a single dispersal event from Australasia to the southern Andes, an implication that fits predictions based on the direction of prevailing winds at southern latitudes (Flemming, 1963, 1979; Raven, 1973; Winkworth et al., 2002b). This is a scenario shared with several other plant groups, e.g. *Coriaria* (Yokoyama et al., 2000), *Drosera* (Rivadavia et al., 2003), the new Zealand hebes (*Veronica*) (Wagstaff et al., 2002) and *Myosotis* (Winkworth et al., 2002a). Overall, the good fit of the cpDNA tree with ecology and with biogeographical patterns across the Indian Ocean and the Pacific lends confidence that a significant level of the species phylogeny is contained within the phylogenetic signal of the plastid tree.

A possible confounding signal of another dimension: geographical patterning of the cpDNA data

While several of the clades within clade F can be characterised based on morphological or ecological characters, those within clade G generally can not (Fig. 3A). The existence of a geographical structure to the cpDNA data, such that samples show affinity according to geographical area of origin rather than to morphology and thus traditional systematic arrangement, could confuse patterns at morphological and ecological levels (Fuertes Aguilar et al., 1999a; Feliner et al., 2004). Geographical patterning in cpDNA markers has been reported for the Tasmanian eucalypts (McKinnon et al., 2001; McKinnon et al., 2004), for Iberian species of *Phlomis* (Albaladejo et al., 2005) and for white oaks in Europe (Dumolin-Lapégue et al., 1997; Petit et al., 2002). In these plant groups there is mounting evidence for the presence of several haplotypes within a single species, shared among species within geographical regions, with introgression and hybridisation being invoked as the most likely cause (Dumolin-Lapégue et al., 1997, Steane et al., 1998, Fuertes Aguilar et al., 1999a, Jackson et al., 1999, McKinnon et al., 2001; Petit et al., 2002). Given that the species in the present analysis hybridise in nature (Brock and Brown, 1961, Spies et al., 1992, Visser and Spies, 1994a-d; Waters, 2007), the occurrence of several ploidy forms within a single species, haplotype sharing among species from the same area (Waters, 2007; Waters et al., 2008) and continuous variation in morphological characters among several species, geographical patterning could offer an explanation to some of the patterns evident in the plastid tree presented here (Fig. 3B, Table 5). For example, such patterning might explain the difficulty to distinguish subclades within clade G and could perhaps account for the separation of one of the accessions of *A. pilosa* from the other two, the grouping of all of the specimens of *R. nivicolum* and *R. nudiflorum* from Tasmania separate from two accessions from other areas, or the grouping of *A. bipartita*, a species found in dry habitats, with accessions of other species from the same area in a clade of otherwise wet-dwellers (Fig. 3). But geographical patterning does not explain the highly disparate phylogenetic positions of the two accessions of *J. pallida* and *A. caespitosa* (Fig. 3), which do not all group with other accessions from the same area. Indeed, our sampling is not sufficiently detailed to rule out alternative explanations such as convergent evolution or lineage sorting and, in addition, the occurrence of long distance dispersal of caryopses would clutter a clear geographical structure to the cpDNA data (Feliner et al., 2004). Bearing this in mind we are, at this stage, forced to conclude that aspects of this phylogeny remain enigmatic and that its resolution would require denser sampling, at the population level, and of the nuclear genome in addition. Despite this, we are confident that evidence from morphology, ecology and distribution indicates that the level of resolution of the plastid tree is sufficient to serve as a framework for a reconsideration of the generic classification.

Implications for a generic classification of *Rytidosperma* s.l.

The three major clades among which the Australasian taxa are distributed reveal a certain amount of agreement with the generic system of Linder and Verboom (1996). Clades E and F are entirely or largely made up of species of *Rytidosperma* and clade G is largely a clade of *Austrodanthonia* species. This pattern probably reflects the ecological component of these genera, but none of the clades bears any resemblance to Zotov's (1963) sections (*Buchanania*, *Semiannularia*, *Notodanthonia*) within his genus *Notodanthonia*, although they were described to explicitly reflect the ecological niches of the species. Placement of *Erythranthera*, *Monostachya* and *Pyrrhanthera* within *Rytidosperma* and *Urochlaena* within *Tribolium* (Linder and Verboom, 1996; Linder and Davidse, 1997) is consistent with their positions in the plastid tree. However, none of the genera *sensu* Linder and Verboom (1996) is monophyletic and

the species of *Notodanthonia* and *Joycea* are scattered in both clades F and G. Constraining each of the four genera of Linder and Verboom (1996) to be monophyletic results in trees significantly longer than would be expected to be the result of stochasticity in the course of molecular evolution and is instead interpreted as the result of the existence of a phylogenetic signal that is incompatible with the present generic system. Significantly different signals contained in the morphological and plastid topologies means morphology alone is not predictive of phylogeny (in this case, plastid tree) and basing classifications entirely on morphology could have led to the taxonomic chaos found in *Rytidosperma* s.l. Indeed, the fact that several clades lack straightforward diagnosis (Fig. 3A) means that subdivision of *Rytidosperma* s.l. into genera would not be

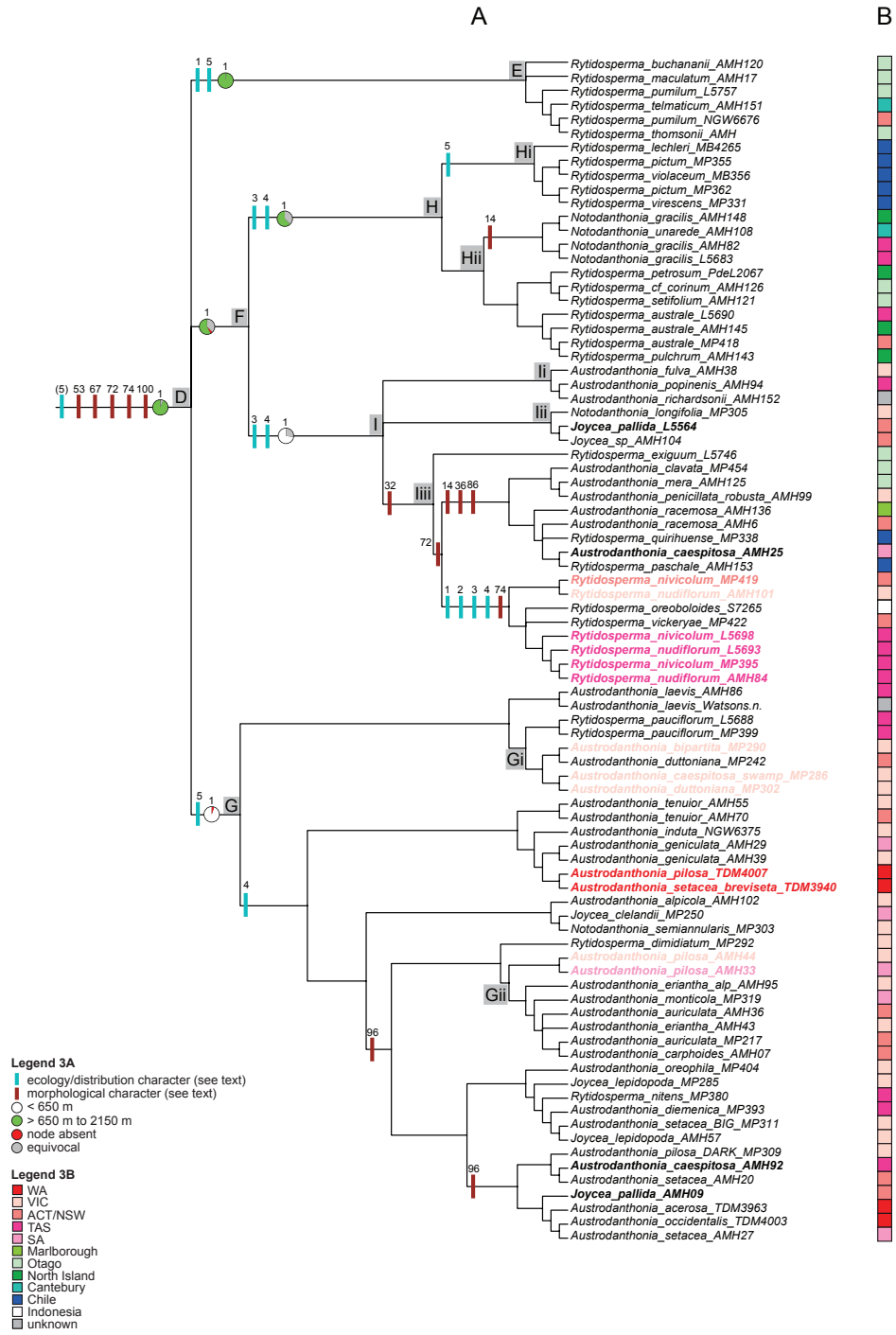

Figure 3. Summary cladogram of *Rytidosperma* s.l. showing (A) what morphological, ecological and distribution characters clades are based on (following parsimony optimisation), parsimony ancestral state reconstruction of the altitude character and (B) collection locality of each sample. Clades correspond to those in Fig. 1, where support values and branch lengths are shown. Branch lengths in this figure have no significance. **A.** Ecological/geographical characters that define a clade are marked with a green bar and morphological characters that define a clade are marked with a red bar. Numbers above the bars correspond to characters listed in Table 3 and Appendix B, respectively. Characters that are listed more than once are represented by different states in different clades. Ecological/distributional: 1. highland, 2. grassland in full sun, 3. basalts [clade H], shales [clade I], granite [within clade Iiii], 4. wet [clades H and within Iiii], dry [clades I and within G], 5. New Zealand [clade E], South America [clade Hi], Australia [clade G], ('Southern Hemisphere-except-Africa' [clade D]). Morphological: 14. innovation buds extravaginal [within clades Hii and Iiii], 32. inflorescences racemose as opposed to paniculate [clade Iiii], 36. pedicels and spikelets parallel to inflorescence axis as opposed to diverging from it [within clade Iiii], 53. callus wider than rachilla internode [clade D], 67. lemma indumentum aggregated into discrete tufts [clade D], 72. presence of upper row of lemma hair [clade D], upper row of lemma hair incomplete [within clade Iiii], 74. presence of lower row of lemma hair [clade D], lower row of lemma hairs in marginal tufts [in clade Iiii], 86. setae exerted from the glumes [within clade Iiii], 96. palea broad [in clade G, but narrow, broad or linear at more inclusive clade], 100. palea keel indumentum ciliate (as opposed to scabrid or absent) [clade D]. Altitude: the optimisation for this character (1) is shown as circles for key clades mentioned in the text. **B.** Geographical origin of each sample for chloroplast data used in this study (based on collection locality, Table 5). WA = Western Australia, VIC = Victoria, ACT/NSW = Australian Capital Territory/New South Wales, TAS = Tasmania, SA = South Australia.

straightforward. Verboom et al. (2006) discussed the implications of recognising the entire *Rytidosperma* clade at generic rank. This large genus would be defined by having a punctate-ovate hilum, a synapomorphy for the clade. An alternative solution is to recognise segregate genera in Africa, but to make of the Australasian and South American species (clade D) a single genus (Linder et al., submitted for publication). This clade can be diagnosed (Fig. 3A) and comprises a group that has been recognised as a coherent entity in the past (with the exclusion of varying treatment of *Erythranthera*, *Pyrrhanthera* and *Monostachya*). Even upon segregation of smaller genera Linder and Verboom (1996) acknowledged that the case for recognising a single, large genus *Rytidosperma* was almost as strong. The main reason not to follow that course then was the nested position of *Karroochloa* within the Australasian species. The current topology removes that reason. Combining the species in clade D into *Rytidosperma* s.l. would create a genus that can be diagnosed by a punctiform hilum, a wide callus, ciliate indumentum on the palea keel, a tri-lobed lemma with a well developed central awn that is often twisted and tufted lemma hairs that are organised in two transverse rows (Fig. 3A), the latter being an aspect that goes back to Steudel's (1854) original concept of the genus. In South America *Rytidosperma* is clearly distinct from other widespread danthonioid genera, *Cortaderia* and *Danthonia*, and in New Zealand it is clearly distinct from *Cortaderia* and *Chionochloa*. In Australia the broader delimitation would not affect communication using the common name (wallaby grasses), as it is used for species in both *Austrodanthonia* and *Rytidosperma* s.s., and would make *Rytidosperma* s.l. the most widespread danthonioid genus in Australia, extending also to Southeast Asia. Recognition of *Rytidosperma* s.l. is thus taxonomically and nomenclaturally conservative and fits a concept still in working use in South America (Baeza, 1996, 2002) and New Zealand (Edgar and Connor, 2000), bar the inclusion of *Pyrrhanthera*.

If we accept a return to Steudel's (1854) genus in an act not so controversial given taxonomic use today, why then was Steudel's genus ever abandoned? The concept of *Rytidosperma* was in fact laid down by Desvaux (1854) when he separated the species of *Danthonia* into two sections based on the length of the callus relative to the rachilla and the arrangement of the hairs of the lemma. Steudel (1854) formalised

these differences at the generic rank, but Bentham doubted the validity of the genus Rytidosperma because it was named after the presence of wrinkled seeds, which turned out to be larvae that had infected the florets of the specimen upon which it was based (Bentham, 1882; Nicora, 1973). Despite the unfortunate name, the concept of *Rytidosperma* was not based solely upon (erroneous) seed characters but the generally degraded state of the type specimen rendered it difficult to place taxonomically for a long time. In fact, Bentham (1882) placed it with *Deschampsia cespitosa* (Pooideae) where it remained until Nicora (1973) revived the name *Rytidosperma* after realising that Zotov's *Notodanthonia* and Steudel's *Rytidosperma* referred to the same taxon (Connor and Edgar, 1979).

A return to a broader concept of *Rytidosperma* is thus in line with Steudel and Zotov, conceptually if not nomenclaturally, deviating only in the inclusion of *Erythranthera* and *Pyrrhanthera*, now believed to constitute morphological oddities embedded within the genus, and in the extension of their generic concepts to include also the New Guinean species including *Monostachya*. A broader concept of *Rytidosperma* is also in line with the wider taxonomic community, where molecular phylogenetic analysis and large scale study seem to be spurring a marked trend toward the recognition of more broadly construed genera (Humphreys and Linder, 2009). A broadly delimited *Rytidosperma* is based on a well supported clade, which we anticipate will be robust to possible phylogenetic reshufflings within the genus, ensuring stability at the generic rank. We hope that compliance with history, common names and contemporary thought will lead to widespread acceptance of the proposed generic delimitation and hence confer its stability.

Conclusion

We present a phylogenetic hypothesis for *Rytidosperma* s.l. based on cpDNA. We conclude that despite relying on a single genome we are able to trace a phylogenetic signal that is supported by morphological, ecological and distribution data and that is sufficient to serve as a framework upon which to base a taxonomic revision of this group at the generic rank. All Australasian and South American species form a well supported clade that can be diagnosed by lemma, caryopsis and palea characters and which is equivalent to Steudel's (1854) concept of the genus *Rytidosperma*. We thus propose reduction to synonymy of *Austrodanthonia*, *Joycea* and *Notodanthonia* and recognition of a broader concept of the genus *Rytidosperma*. Formal taxonomic changes, including further changes across the Danthonioideae as a whole, will be made in a separate paper (Linder et al., submitted for publication).

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Appendix A. Accessions table. Accessions in bold were generated for this study.

			non-coding markers				coding markers						
Name	Voucher (herbarium)	Locality	trnLF	rpl16	atpB-rbcL	ITS	trnT-L	trnD-psbM	psbM-yof6	yof6-trnC	rbcL	ndhF	matK
Austrodanthonia acerosa (Vickery) H.P.Linder	Macfarlane, T.D. 3963 (PERTH)	AU, WA, Lake Unicup	GQ471744	GQ471707	GQ471068		GQ471325	GQ471220	GQ471123	GQ471443		GQ471578	
Austrodanthonia alpicola (Vickery) H.P.Linder	Humphreys, A.M. 102 (Z)	AU, VIC, Mt. Cope	EU401113	EU400961	EU400825	EU401260	GQ471326	GQ471221	GQ471124	GQ471444	GQ471676	GQ471579	GQ471550
Austrodanthonia auriculata (J.M.Black) H.P.Linder	Humphreys, A.M. 36 (Z)	AU, SA, Waite Reserve	EU401114	EU400962	EU400826		GQ471327	GQ471222	GQ471125	GQ471445		GQ471580	
Austrodanthonia auriculata (J.M.Black) H.P.Linder	Pirie, M.D. 217 (Z)	AU, ACT, Mt. Ainslie	EU401115	EU400963	GQ471069	EU401261	GQ471328	GQ471223	GQ471126	GQ471446		GQ471581	
Austrodanthonia bipartita (Kunth) H.P.Linder	Pirie, M.D. 290 (Z)	AU, VIC, Grampians National Park	EU400115	EU400963	EU400827	EU401261	GQ471329	GQ471224	GQ471127	GQ471447	GQ471677	GQ471582	
Austrodanthonia caespitosa (R.Br.) H.P.Linder	Humphreys, A.M. 25 (Z)	AU, SA, Truro	EU401116	EU400964	EU400828	EU401262	GQ471330	GQ471225	GQ471128	GQ471448	GQ471678	GQ471583	GQ471551
Austrodanthonia caespitosa (R.Br.) H.P.Linder	Humphreys, A.M. 92 (Z)	AU, TAS, Gravelly Beach	EU401117	EU400965	EU400829	EU401263	GQ471331	GQ471226	GQ471129	GQ471449	GQ471679	GQ471584	GQ471552
Austrodanthonia caespitosa 'swamp'	Pirie, M.D. 286 (Z)	AU, VIC, Grampians National Park	GQ471745	GQ471708	GQ471071		GQ471332	GQ471227	GQ471130	GQ471450			
Austrodanthonia carphoides (Benth.) H.P.Linder	Humphreys, A.M. 7 (Z)	AU, ACT, Namadgi National Park		GQ471709	GQ471072		GQ471333	GQ471228	GQ471131	GQ471451		GQ471585	
Austrodanthonia carphoides (Benth.) H.P.Linder	Linder, H.P. 5568 (CHR)	AU, ACT, Black Mt.	EU401118	EU400966		EU401264	GQ471334	GQ471229	GQ471132	GQ471452	EU400653	EU400770	EU400714
Austrodanthonia clavata (Zotov) H.P.Linder	Pirie, M.D. 454 (Z)	NZ, Otago, Pisa range	EU401119	EU400967	EU400830	EU401265	GQ471335	GQ471230	GQ471133	GQ471453	GQ471680	GQ471586	GQ471553
Austrodanthonia diemenica (D.I.Morris) H.P.Linder	Pirie, M.D. 393 (Z)	AU, TAS, Walls of Jerusalem National Park			GQ471074		GQ471336						
Austrodanthonia duttoniana (Cashmore) H.P.Linder	Pirie, M.D. 242 (Z)	AU, NSW, Sturt Hwy		GQ471710	GQ471075		GQ471337	GQ471231	GQ471134	GQ471454	GQ471681	GQ471587	GQ471554
Austrodanthonia duttoniana (Cashmore) H.P.Linder	Pirie, M.D. 302 (Z)	AU, VIC, Calder Hwy	EU401120	EU400968	EU400831	EU401266	GQ471338	GQ471232	GQ471135	GQ471455		GQ471588	
Austrodanthonia eriantha 'alp'	Humphreys, A.M. 95 (Z)	AU, VIC, Mt. Buffalo National Park	EU401122	EU400970	EU400833	EU401267	GQ471339	GQ471233	GQ471136	GQ471456		GQ471589	
Austrodanthonia eriantha (Lindl.) H.P.Linder	Humphreys, A.M. 43 (Z)	AU, VIC, Grampians National Park	EU401121	EU400969	EU400832	GQ471540	GQ471340	GQ471234	GQ471137	GQ471457	GQ471682	GQ471590	GQ471555
Austrodanthonia fulva (Vickery) H.P.Linder	Humphreys, A.M. 38 (Z)	AU, VIC, Grampians National Park	EU401123	EU400971	EU400834	EU401268	GQ471341	GQ471235	GQ471138	GQ471458	GQ471683	GQ471591	GQ471556
Austrodanthonia geniculata (J.M.Black) H.P.Linder	Humphreys, A.M. 29 (Z)	AU, SA, Mt. Barker	GQ471746	GQ471711	GQ471076		GQ471342	GQ471236	GQ471139	GQ471459		GQ471592	
Austrodanthonia geniculata (J.M.Black) H.P.Linder	Humphreys, A.M. 39 (Z)	AU, VIC, Grampians National Park	EU401124	EU400972	EU400835	GQ471541	GQ471343	GQ471237	GQ471140	GQ471460	GQ471684	GQ471593	
Austrodanthonia induta (Vickery) H.P.Linder	Walsh, N.G. 6375 (Z)	AU, VIC, Grampians National Park	EU401125	EU400973	EU400836	EU401269	GQ471344	GQ471238	GQ471141	GQ471461		GQ471594	
Austrodanthonia laevis (Vickery) H.P.Linder	Humphreys, A.M. 86 (Z)	AU, TAS, Gowrie Park	GQ471747	GQ471712	GQ471077		GQ471345	GQ471239	GQ471142	GQ471462	GQ471685	GQ471595	GQ471557
Austrodanthonia laevis (Vickery) H.P.Linder	Watson, L. *s.n.* (ANU)	Australia	EU401126	EU400974	EU400837	AF019875	GQ471346	GQ471240	GQ471143	GQ471463		GQ471596	
Austrodanthonia mera (Connor & Edgar) H.P.Linder	Humphreys, A.M. 125 (Z)	NZ, Otago, Richardson Mts.	EU401127	EU400975	EU400838	EU401270	GQ471347	GQ471241	GQ471144	GQ471464	EU400654	EU400771	EU400715
Austrodanthonia monticola (Vickery) H.P.Linder	Pirie, M.D. 319 (Z)	AU, NSW, Hume Hwy	EU401128	EU400976	EU400839	EU401271	GQ471348	GQ471242	GQ471145	GQ471465		GQ471597	
Austrodanthonia occidentalis (Vickery) H.P.Linder	Macfarlane, T.D. 4003 (PERTH)	AU, WA, Broke Inlet	GQ471748	GQ471713	GQ471079		GQ471349	GQ471243	GQ471146	GQ471466		GQ471598	
Austrodanthonia oreophila (H.P.Linder & N.G. Walsh) H.P.Linder	Pirie, M.D. 404 (Z)	AU, VIC, Mt. Buffalo National Park	EU401129	EU400977	EU400840	EU401272	GQ471350	GQ471244	GQ471147	GQ471467		GQ471599	
Austrodanthonia penicillata (Labill.) H.P.Linder	Humphreys, A.M. 68 (Z)	AU, NSW, Blue Mts	GQ471749		GQ471080		GQ471351						
Austrodanthonia penicillata (Labill.) H.P.Linder	Humphreys, A.M. 87 (Z)	AU, TAS, Gowrie Park	GQ471750		GQ471081		GQ471352						
Austrodanthonia penicillata 'robusta'	Humphreys, A.M. 99 (Z)	AU, VIC, Bogong Highplains	EU401130	EU400978	EU400841	EU401273	GQ471353	GQ471245	GQ471148	GQ471468		GQ471600	
Austrodanthonia pilosa (R.Br.) H.P.Linde	Humphreys, A.M. 44 (Z)	AU, VIC, Grampians National Park	EU401131	EU400979	EU400842	EU401274	GQ471354	GQ471246	GQ471149	GQ471469		GQ471601	
Austrodanthonia pilosa 'dark'	Pirie, M.D. 309 (Z)	AU, VIC, Bungalook Conservation Reserves	GQ471751	GQ471714	GQ471082		GQ471355	GQ471247	GQ471150	GQ471470		GQ471602	
Austrodanthonia pilosa pilosa (R.Br.) H.P.Linder	Humphreys, A.M. 34 (Z)	AU, SA, Waite Reserve	GQ471752	GQ471715	GQ471083		GQ471356	GQ471248	GQ471151	GQ471471		GQ471603	
Austrodanthonia pilosa (R.Br.) H.P.Linder	Macfarlane, T.D. 4007 (PERTH)	AU, WA, Quilben Rd.	GQ471753	GQ471716	GQ471084		GQ471357	GQ471249	GQ471152	GQ471472		GQ471604	
Austrodanthonia popinensis (D.I.Morris) H.P.Linder	Humphreys, A.M. 94 (Z)	AU, TAS, Midland Hwy	EU401132	EU400980	EU400843	EU401275	GQ471358	GQ471250	GQ471153	GQ471473		GQ471605	
Austrodanthonia racemosa (R.Br.) H.P.Linder	Humphreys, A.M. 136 (Z)	NZ, Marlborough, Karaka Scenic Reserve	GQ471754	GQ471717	GQ471086	GQ471542	GQ471359	GQ471251		GQ471474		GQ471606	
Austrodanthonia racemosa (R.Br.) H.P.Linder	Humphreys, A.M. 6 (Z)	AU, ACT, Namadgi National Park	EU401133	EU400981	EU400844	EU401276	GQ471360	GQ471252	GQ471154	GQ471475	GQ471686	GQ471607	GQ471558
Austrodanthonia racemosa (R.Br.) H.P.Linder	Humphreys, A.M. 91 (Z)	AU, TAS, Gravelly Beach		GQ471718	GQ471086	GQ471543		GQ471253	GQ471155				
Austrodanthonia richardsonii (Cashmore) H.P.Linder	USDA PI 202162 (voucher: Humphreys, A. 152) (Z)	Australia	EU401134	GQ471719	EU400845	EU401277	GQ471361	GQ471254	GQ471156	GQ471476		GQ471608	
Austrodanthonia setacea (R.Br.) H.P.Linder	Humphreys, A.M. 20 (Z)	AU, NSW, Sturt Hwy	EU401135	EU400982	EU400846	EU401278	GQ471362	GQ471255	GQ471157	GQ471477		GQ471609	
Austrodanthonia setacea (R.Br.) H.P.Linder	Humphreys, A.M. 27 (Z)	AU, SA, Mt. Barker town	GQ471755	GQ471720	GQ471088		GQ471363	GQ471256	GQ471158	GQ471478	GQ471687	GQ471610	GQ471559
Austrodanthonia setacea 'big '	Pirie, M.D. 311 (Z)	AU, VIC, Bungalook Conservation Reserves	GQ471756	GQ471721	GQ471089		GQ471364	GQ471257	GQ471159	GQ471479		GQ471611	
Austrodanthonia setacea 'breviseta'	Macfarlane, T.D. 3940 (PERTH)	AU, WA, Lake Chinocup	GQ471757	GQ471722	GQ471090		GQ471365	GQ471258	GQ471160	GQ471480		GQ471612	
Austrodanthonia sp. Goomalling	Clarke, S. 212 (PERTH)	AU, WA, Quairading	GQ471758	GQ471723	GQ471091		GQ471366	GQ471259	GQ471161	GQ471481		GQ471613	
Austrodanthonia tenuior (Steud.) H.P.Linder	Humphreys, A.M. 55 (Z)	AU, VIC, William Morris Reserve	GQ471759	GQ471724	GQ471092		GQ471367	GQ471260	GQ471162	GQ471482	GQ471688	GQ471614	
Austrodanthonia tenuior (Steud.) H.P.Linder	Humphreys, A.M. 70 (Z)	AU, NSW, Blue Mts	EU401136	EU400983	EU400847	EU401279	GQ471368	GQ471261	GQ471163	GQ471483		GQ471615	
Cortaderia fulvida Buchanan (Zotov)	G 5088 (BOL)	NZ, Lincoln	EU401167	EU401012	EU400874	AF367615	GQ471369	GQ471262			DQ887102	EU400780	EU400724
Danthonia alpina Vest.	Pirie, M.D. 480 (Z)	CH, Ticino, Mt. San Giorgio	EU401181	EU401026	EU400880	EU401302	GQ471370				EU400660	EU400783	EU400727
Danthonia cumminsii Hook.f.	Soreng, R.J. 5638 (US)	CHN, Xizhang, Tibet	EU401194	EU401036	EU400884	DQ887161	GQ471371				DQ887103	EU400787	EU400731
Joycea clelandii (Vickery) H.P.Linder	Pirie, M.D. 250 (Z)	AU, SA, Mt. Barker town	EU401200	EU401039	EU400887	EU401314	GQ471372	GQ471263	GQ471164	GQ471484		GQ471616	
Joycea lepidopoda (N.G.Walsh) H.P.Linder	Humphreys, A.M. 57 (Z)	AU, VIC, Baluk William Reserve	GQ471760	GQ471725	GQ471094		GQ471373	GQ471264	GQ471165	GQ471485		GQ471617	
Joycea lepidopoda (N.G.Walsh) H.P.Linder	Pirie, M.D. 285 (Z)	AU, VIC, Grampians National Park	EU401201	EU401040	EU400888	EU401315	GQ471374	GQ471265	GQ471166	GQ471486	EU400665	EU400790	EU400734
Joycea pallida (R.Br.) H.P.Linder	Humphreys, A.M. 9 (Z)	AU, ACT, Mulligan's Flat	GQ471761	GQ471726	GQ471095		GQ471375	GQ471266	GQ471167	GQ471487	GQ471689	GQ471618	GQ471560
Joycea pallida (R.Br.) H.P.Linder	Linder, H.P. 5564 (CANB)	AU, ACT, Black Mt.	DQ218160		EU400889	F019880; DQ2181	GQ471376	GQ471267	GQ471168	GQ471488		GQ471619	
Joycea sp.	Humphreys, A.M. 104 (Z)	AU, NSW, Budawang National Park	EU401202	EU401041	EU400890	EU401316	GQ471377	GQ471268	GQ471169	GQ471489	GQ471690	GQ471620	GQ471561
Karroochloa curva (Nees) Conert & Tuerpe	Verboom, G.A. 604 (BOL)	S. Africa, Malgas.	DQ218163	EU401042	EU400891	DQ218200	GQ471378	GQ471269	GQ471170	GQ471490	EU400666	EU400791	EU400735
Karroochloa curva (Nees) Conert & Tuerpe	Verboom, G.A. 626 (BOL)	S. Africa, McGregor	DQ218164	GQ471727		DQ218201	GQ471379					GQ471621	
Karroochloa purpurea (L.f.) Conert & Tuerpe	Verboom, G.A. 603 (BOL)	S. Africa, Malgas.	DQ218161			DQ218198						GQ471622	
Karroochloa schismoides (Stapf ex Conert) Conert & Tuerpe	Verboom, G.A. 562 (BOL)	Namibia, Rosh Pinah	DQ218165	EU401043	EU400892	DQ218202	GQ471380	GQ471270	GQ471171	GQ471491	EU400667	EU400792	EU400736
Karroochloa schismoides (Stapf ex Conert) Conert & Tuerpe	Verboom, G.A. 569 (BOL)	S. Africa, Steinkopf	DQ218166	GQ471728	GQ471096	DQ218203	GQ471381		GQ471172	GQ471492		GQ471623	
Karroochloa tenella (Nees) Conert & Tuerpe	Verboom, G.A. 587 (BOL)	S. Africa, Vanrhynsdorp	DQ218162	EU401044	EU400893	DQ218199	GQ471382	GQ471271			GQ471691	GQ471624	GQ471562
Lamprothyrsus peruvianus Hitchc.	G 11154 (BOL)	NZ, ex. cult	EU401204	EU401046	EU400894	AF367605	GQ471383	GQ471272			DQ887105	EU400793	EU400737
Merxmuellera aureocephala (J.G.Anders.) Conert	Barker, N.P. 1816 (GRA)	S. Africa, Bushmans Nek	EU401207	EU401048	EU400896	GQ471544		GQ471273	GQ471173	GQ471493			
Merxmuellera disticha (Nees) Conert	Barker, N.P. 1002 (BOL)	S. Africa, Nieu Bethesda	EU401052	EU400899	F367600; AF0198		GQ471384	GQ471274	GQ471174	GQ471494	DQ887109	EU400797	EU400741
Merxmuellera dura (Stapf) Conert	Barker, N.P. 983 (BOL)	S. Africa, Nieuwoudville Wild Flower Reserve	DQ218190	EU401054	EU400901	F019872, DQ2181	GQ471385				DQ887111	EU400799	EU400743

Appendix A. Accessions table. Accessions in bold were generated for this study.

Merxmuellera stricta (Schrad.) Conert	vd Niet, T. 15 (Z)	S. Africa, West Cape	DQ913472	DQ913326	DQ913241	GQ471545	GQ471386				GQ471692	GQ471625	GQ471563
Notodanthonia gracilis (Hook.f.) Zotov	Humphreys, A.M. 148 (Z)	NZ, Hawkes Bay, Ruahine Forest Reserve	EU401221	EU401062	EU400909	EU401322	GQ471387	GQ471275	GQ471175	GQ471495	EU400668	EU400805	EU400749
Notodanthonia gracilis (Hook.f.) Zotov	Humphreys, A.M. 82 (Z)	AU, TAS, Lyle Hwy	GQ471762	GQ471729	GQ471099	GQ471546	GQ471388	GQ471276	GQ471176	GQ471496		GQ471626	
Notodanthonia gracilis (Hook.f.) Zotov	Linder, H.P. 5683 (BOL)	AU, TAS, Franklin River	DQ218158	EU401063	EU400910	F367603; DQ2181	GQ471389	GQ471277	GQ471177	GQ471497	GQ471693	GQ471627	GQ471564
Notodanthonia longifolia (R.Br.) Veldk.	Pirie, M.D. 305 (Z)	AU, VIC, ex. Cult	EU401222	EU401064	EU400911	EU401323	GQ471390	GQ471278			EU400669	GQ471628	GQ471565
Notodanthonia semiannularis (Labill.) Zotov	Pirie, M.D. 303 (Z)	AU, VIC, Racecourse Marshlands Reserve	EU401223	EU401065	EU400912	EU401324	GQ471391	GQ471279	GQ471178	GQ471498	GQ471694	GQ471629	GQ471566
Notodanthonia unarede (Raoul) Zotov	Humphreys, A.M. 108 (Z)	NZ, Canterbury, Banks Peninsula		EU401066	EU400913	EU401325	GQ471392	GQ471280	GQ471179	GQ471499		GQ471630	
Pseudopentameris macrantha (Schrad.) Conert	Linder, H.P. 5470 (BOL)	S. Africa, West Cape, De Hoop	DQ218192	EU401075	EU400919	AF367598	GQ471393				DQ887122	EU400816	EU400760
Rytidosperma australe (Petrie) Connor & Edgar	Humphreys, A.M. 145 (Z)	NZ, Hawkes Bay, Ruahine Forest Reserve	EU401235	EU401077	EU400922	EU401385	GQ471394	GQ471281	GQ471180	GQ471500	GQ471695	GQ471631	GQ471567
Rytidosperma australe (Petrie) Connor & Edgar	Linder, H.P. 5690 (BOL)	AU, TAS, Cradle Mt.	GQ471763	GQ471730	GQ471102		GQ471395	GQ471282	GQ471181	GQ471501		GQ471632	
Rytidosperma australe (Petrie) Connor & Edgar	Pirie, M.D. 418 (Z)	AU, NSW, Kosciuszko National Park	EU401234	EU401078	EU400921	EU401384	GQ471396	GQ471283	GQ471182	GQ471502		GQ471633	EU400762
Rytidosperma buchananii (Hook.f.) Connor & Edgar	Humphreys, A.M. 120 (Z)	NZ, Otago, Richardson Range	EU401236	EU401079	EU400923	EU401386	GQ471397	GQ471284	GQ471183	GQ471503		GQ471634	
Rytidosperma cf corinum Connor & Edgar	Humphreys, A.M. 126 (Z)	NZ, Otago, Richardson Mts.	GQ471764	GQ471731	GQ471103		GQ471398	GQ471285	GQ471184	GQ471504		GQ471635	
Rytidosperma dimidiatum (Vickery) Connor & Edgar	Pirie, M.D. 292 (Z)	AU, VIC, Grampians National Park	EU401237	EU401080	EU400924	EU401387	GQ471399	GQ471286	GQ471185	GQ471505		GQ471636	
Rytidosperma exiguum (Kirk) H.P.Linder	Linder, H.P. 5746 (CHR)	NZ, Otago, Mt. Somers	EU401238	EU401081	EU400925	EU401388	GQ471400	GQ471287	GQ471186	GQ471506	GQ471696	GQ471637	GQ471568
Rytidosperma fortunae-hibernae (Renvoize) Connor & Edgar	Humphreys, A.M. 73 (Z)	AU, TAS, Mt. Field National Park	EU401239	EU401082	EU400926	EU401389	GQ471401	GQ471288	GQ471187	GQ471507		GQ471638	
Rytidosperma lechleri Steud.	Baeza, C.M. 4256 (CONC)	CHL, VIII Región, Ñuble	EU401239	EU401082	EU400926	EU401389	GQ471402	GQ471289	GQ471188	GQ471508	EU400672	EU400818	EU400763
Rytidosperma maculatum (Zotov) Connor & Edgar	Humphreys, A.M. 117 (Z)	NZ, Otago, Carrick Range	EU401241	EU401084	EU400928	EU401391	GQ471403	GQ471290	GQ471189	GQ471509	EU400673	EU400819	EU400764
Rytidosperma nitens (D.I.Morris) H.P.Linder	Pirie, M.D. 380 (Z)	AU, TAS, Franklin River	EU401242	EU401085	EU400929	EU401392	GQ471404	GQ471291	GQ471190	GQ471510		GQ471639	
Rytidosperma nivicolum (Vickery) Connor & Edgar	Linder, H.P. 5698 (BOL)	AU, TAS, Mother Lords Plain	GQ471766	GQ471732	GQ471105	GQ471547	GQ471405	GQ471292	GQ471191	GQ471511		GQ471640	
Rytidosperma nivicolum (Vickery) Connor & Edgar	Pirie, M.D. 395 (Z)	AU, TAS, Walls of Jerusalem National Park	GQ471765	GQ471733	GQ471106		GQ471406	GQ471293	GQ471192	GQ471512		GQ471641	
Rytidosperma nivicolum (Vickery) Connor & Edgar	Pirie, M.D. 419 (Z)	AU, NSW, Kosciuszko National Park	EU401242	EU401085	EU400929	EU401392	GQ471407	GQ471294	GQ471193	GQ471513		GQ471642	
Rytidosperma nudiflorum (P.F.Morris) Connor & Edgar	Humphreys, A.M. 101 (Z)	AU, VIC, Bogong Highplains	GQ471767	GQ471734	GQ471107	GQ471548	GQ471408	GQ471295	GQ471194	GQ471514		GQ471643	
Rytidosperma nudiflorum (P.F.Morris) Connor & Edgar	Humphreys, A.M. 84 (Z)	AU, TAS, Vale River	GQ471768	GQ471735	GQ471108		GQ471409	GQ471296	GQ471195	GQ471515		GQ471644	
Rytidosperma nudiflorum (P.F.Morris) Connor & Edgar	Linder, H.P. 5693 (BOL)	AU, TAS, Cradle Mt.	DQ218159	EU401087	EU400931	F019876; DQ2181	GQ471410	GQ471297	GQ471196	GQ471516	GQ471697	GQ471645	GQ471569
Rytidosperma oreoboloides (F.Muell.) H.P.Linder	Sands MWC8877-7265 (K)	INDO, Irian Jaya	EU401244	EU401088	EU400932	DQ887179		GQ471298	GQ471197	GQ471517		GQ471646	
Rytidosperma paschale (Pilg.) C.M.Baeza	Zizka, F. cult. (voucher: Humphreys, A.M. 153) (Z)	CHL, Easter Island, ex. Cult	EU401245	EU401089	EU400933	EU401394	GQ471411	GQ471299	GQ471198	GQ471518	GQ471698	GQ471647	GQ471570
Rytidosperma pauciflorum (R.Br.) Connor & Edgar	Linder, H.P. 5688 (Z)	AU, TAS, Cradle Mt.	EU401246	EU401090	EU400934	EU401395	GQ471412	GQ471300	GQ471199	GQ471519		GQ471648	
Rytidosperma pauciflorum (R.Br.) Connor & Edgar	Pirie, M.D. 399 (Z)	AU, TAS, Walls of Jerusalem National Park	GQ471769	GQ471736	GQ471110		GQ471413	GQ471301	GQ471200	GQ471520	GQ471699	GQ471649	GQ471571
Rytidosperma petrosum Connor & Edgar	Lange, de P.J. 2067 (AK)	NZ, Wellington, Cape Palliser	GQ471770	GQ471737	GQ471111	AY752480	GQ471414	GQ471302				GQ471650	
Rytidosperma pictum pictum (Nees & Meyen) Nicora	Pirie, M.D. 355 (Z)	CHL, VIII Región, Biobio	EU401247	EU401091	EU400935	EU401396	GQ471415	GQ471303	GQ471201	GQ471521	EU400674	EU400820	EU400765
Rytidosperma pictum pictum (Nees & Meyen) Nicora	Pirie, M.D. 362 (Z)	CHL, VIII Región, Biobio	GQ471771	GQ471738	GQ471112	GQ471549	GQ471416	GQ471304	GQ471202	GQ471522		GQ471651	
Rytidosperma pulchrum Zotov (Connor & Edgar)	Humphreys, A.M. 143 (Z)	NZ, Hawkes Bay, Ruahine Forest Reserve	EU401248	EU401092	EU400936	EU401397	GQ471417	GQ471305	GQ471203	GQ471523		GQ471652	
Rytidosperma pumilum (Kirk) Clayton & Renvoize ex Connor & Edgar	Linder, H.P., 5747 (Z)	NZ, Otago, Mt. Somers	EU401249	GQ471739	EU400937	AF019878	GQ471418	GQ471306	GQ471204	GQ471524	GQ471700	GQ471653	GQ471572
Rytidosperma pumilum (Kirk) Clayton & Renvoize ex Connor & Edgar	Walsh, N.G. 6676 (MEL)	AU, NSW, Southern Tablelands	EU401250	EU401092	EU400938	EU401398	GQ471419	GQ471307	GQ471205	GQ471525	GQ471701	GQ471654	GQ471573
Rytidosperma quirihuense C.M.Baeza	Pirie, M.D. 338 (Z)	CHL, VIII Región, Concepción	EU401251	EU401093	EU400939		GQ471420	GQ471308			GQ471702	GQ471655	GQ471574
Rytidosperma setifolium (Hook.f.) Connor & Edgar	Humphreys, A.M. 121 (Z)	NZ, Otago, Richardson Range	EU401252	EU401094	EU400940	EU401400	GQ471421	GQ471309	GQ471206	GQ471526	GQ471703	GQ471656	GQ471575
Rytidosperma telmaticum Connor & Molloy	Humphreys, A.M. 151 (Z)	NZ, Canterbury, Lake Heron	EU401253	EU401095	EU400941	EU401401	GQ471422	GQ471310	GQ471207	GQ471527	GQ471704	GQ471657	GQ471576
Rytidosperma thomsonii (Buchanan) Connor & Edgar	Humphreys, A.M. 118 (Z)	NZ, Otago, Richardson Range	EU401254	EU401096	EU400942	EU401402	GQ471423	GQ471311	GQ471208	GQ471528	EU400675	EU400821	EU400766
Rytidosperma vestitum (Pilg.) Connor & Edgar	Marsden, K. 132 (K)	INDO, Irian Jaya	EU401255	EU401097	EU400943	DQ887180		GQ471312				GQ471658	
Rytidosperma vickeryae Gray & H.P.Linder	Pirie, M.D. 422 (Z)	AU, NSW, Kosciuszko National Park	EU401256	EU401098	EU400944	EU401403	GQ471424	GQ471313	GQ471209	GQ471529		GQ471659	
Rytidosperma violaceum (Desv.) Nicora	Pirie, M.D. 356 (Z)	CHL, VIII Región, Biobio	EU401257	EU401099	EU400945	EU401404	GQ471425	GQ471314	GQ471210	GQ471530		GQ471660	
Rytidosperma virescens (Desv.) Nicora	Pirie, M.D. 331 (Z)	CHL, VIII Región, Ñuble	EU401258	EU401100	EU400946	EU401405	GQ471426	GQ471315	GQ471211	GQ471531		GQ471661	
Schismus arabicus Nees	Willis, J.H. *s.n.* (MEL)	AU, WA, Coolgardie	EU401259		EU400947		GQ471427					GQ471662	
Schismus barbatus (Leofl. Ex L.) Thell.	Verboom, G.A. 503 (BOL)	S. Africa, Leopoldtville	DQ218167	EU401101	EU400948	DQ218204	GQ471428	GQ471316	GQ471212	GQ471532	EU400676	EU400822	EU400767
Schismus barbatus (Leofl. Ex L.) Thell.	Verboom, G.A. 572 (BOL)	S. Africa, Springbok	DQ218168	GQ471740	GQ471114	DQ218205	GQ471429	GQ471317				GQ471663	
Schismus pleuropogon Stapf.	Verboom, G.A. 628 (BOL)	S. Africa, McGregor	DQ218187	EU401102	EU400949	DQ218222	GQ471430				GQ471705	GQ471664	GQ471577
Schismus scaberrimus Nees	Verboom, G.A. 573 (BOL)	S. Africa, Kamiesberg	DQ218169	EU401103	EU400950	DQ218206	GQ471431					GQ471665	
Schismus scaberrimus Nees	Verboom, G.A. 586 (BOL)	S. Africa, Nieuwoudtville	DQ218170			DQ218207							
Tribolium acutiflorum (Nees) Renvoize	Verboom, G.A. 504 (BOL)	S. Africa, Aurora	DQ218186	EU401104	EU400951	DQ218221	GQ471432		GQ471213	GQ471533		GQ471666	
Tribolium brachystachyum (Nees) Renvoize	Verboom, G.A. 593 (BOL)	S. Africa, Heldberg	DQ218172	EU401105	EU400952	DQ218209	GQ471433	GQ471318	GQ471214	GQ471534	EU400677	EU400823	EU400768
Tribolium ciliare (Stapf.) Renvoize	Verboom, G.A. 596 (BOL)	S. Africa, De Hoop	DQ218175	EU401106	EU400953	DQ218211	GQ471434				GQ471706	GQ471667	
Tribolium echinatum (Thunb.) Renvoize	Verboom, G.A. 576 (BOL)	S. Africa, Kamieskroon	DQ218176			DQ218212							
Tribolium echinatum (Thunb.) Renvoize	Verboom, G.A. 601 (BOL)	S. Africa, De Hoop	DQ218177	EU401107	GQ471116	DQ218213	GQ471435					GQ471668	
Tribolium hispidum (Thunb.) Renvoize	Verboom, G.A. 532 (BOL)	S. Africa, Cape Peninsula	DQ218178	EU401108	GQ471117	DQ218214	GQ471436					GQ471669	
Tribolium hispidum (Thunb.) Renvoize	Verboom, G.A. 599 (BOL)	S. Africa, De Hoop	DQ218180	GQ471741	GQ471118	DQ218214		GQ471319	GQ471215	GQ471535		GQ471670	
Tribolium obliterum (Hemsl.) Renvoize	Verboom, G.A. 598 (BOL)	S. Africa, De Hoop	DQ218184	EU401109	EU400956	DQ218219	GQ471437	GQ471320	GQ471216	GQ471536		GQ471671	
Tribolium obtusifolium (Nees) Renvoize	Verboom, G.A. 597 (BOL)	S. Africa, De Hoop	DQ218185	EU401110	EU400957	DQ218220	GQ471438					GQ471672	
Tribolium pusillum (Nees) H.P.Linder & Davidse	Verboom, G.A. 554 (BOL)	S. Africa, Vanrhynsdorp	DQ218183	EU401111	EU400958	DQ218218	GQ471439	GQ471321	GQ471217	GQ471537	EU400678	EU400824	EU400769
Tribolium uniolae (L.f.) Revoize	Verboom, G.A. 530 (BOL)	S. Africa, Cape Peninsula	DQ218174	GQ471742	GQ471120	DQ218210	GQ471440	GQ471322	GQ471218	GQ471538		GQ471673	
Tribolium uniolae (L.f.) Revoize	Verboom, G.A. 531 (BOL)	S. Africa, Cape Peninsula	DQ218171	GQ471743	GQ471121	DQ218208	GQ471441	GQ471323				GQ471674	
Tribolium utriculosum (Nees) Renvoize	Verboom, G.A. 568 (BOL)	S. Africa, Steinkopf	DQ218181	EU401112	GQ471122	DQ218216	GQ471442	GQ471324	GQ471219	GQ471539		GQ471675	

Appendix B. Morphological characters and character states.

1. plants < lifeform> (0) annual (1) biennial (2) perennial
2. plants <growthform> (0) caespitose (1) loosely caespitose (2) tangled 3) cushion forming (4) single or several shoots (5) mat- or ring-forming (6) tufted
3. stolons <presence> (0) absent (1) present
4. basal sheath appearance (0) burnt-off leaf-bases forming a sheath (1) white shiny persistent sheaths (2) sheaths brown and soon rotting (3) cauline leaves and no sheaths (4) brown and persistent sheath, often with abscission line from blade (5) brown, persistent, lacerated and curly
5*. old sheaths breaking up or remaining intact (0) remaining intact (1) breaking up into fibres (2) splitting transversely into segments
6*. shoot base swollen or not (0) swollen (1) not swollen
7*. shoot base <indumentum> (0) villous (1) glabrous
8*. prophylls <apical shape> (0) acute (1) truncate, often bilobed (2) V-shaped
9. prophylls <upper margin indumentum (0) glabrous (1) ciliate or bristly (2) woolly
10. prophylls keels <alignment> (0) converging towards the apex (1) remaining parallel to the apex
11*. prophylls <keel indumentum> (0) glabrous (1) scaberulous or dentate (2) ciliate (3) villous
12. prophyllar awns (0) extended as awns (1) not extending beyond the prophyllar apex
13. prophyll awns indumentum (0) smooth (1) scaberulous
14. innovation buds <position> (0) intravaginal (1) extravaginal
15*. culms <geniculate or ascending (0) straight (1) ascending
16. leaves <insertion position> (0) basal (1) cauline (2) radical
17. leaves <indumentum> (0) glabrous (1) scaberulous (2) puberulous (3) pubescent (4) villous (5) hispid
18. leaves indumentum <density> (0) a dense felt (1) shaggy and dense (2) sparse (3) very sparse
19. leaves <indumentum distribution> (0) on whole leaf (1) on sheath-surface (2) on blade-surface (3) on sheath-margins (4) on blade-margins
20. leaf-hairs <simple or tubercle (0) simple (1) tubercle-based
21. sheath mouth <indumentum> (0) glabrous (1) woolly (2) with a ring of bristles (3) villous (4) leaf margins above mouth
22. indumentum on the adaxial leaf (0) absent (1) present, often as a web of interlocking hairs (2) present, as a felt of short hairs
23. leaf blades when fresh <expanded or rolled> (0) expanded (1) rolled (2) margins incurved
24. leaf blades when dry <expanded (0) flat (1) inrolled (2) folded double
25. leaf blades inner surface <ind (0) glabrous (1) villous (2) densely villous (3) woolly (4) puberulous (5) pilose
26. leaf blades <stiffness> (0) rigid (1) flaccid
27. leaf blades <thickness> (0) thick (1) thin
28. leaf blades <apices acute or not> (0) acute (1) aciculate (2) truncate (3) rounded
29. leaf blades <pungent or not> (0) pungent (1) sometimes pungent (2) soft-tipped
30. leaf blades margins <scabridity> (0) smooth (1) scabrid
31. leaf blades when old <persistent> (0) persistent on sheath (1) disarticulating from a persistent sheath
32. inflorescence structure, degree of branching (0) strictly racemose (1) largely racemose, with a few basal branches (2) sparsely paniculate, with only one or two order branches (3) widely paniculate
33. inflorescence secund or not (0) even all round (1) secund
34. inflorescence open or contracted (0) open (1) contracted (2) spikelike (3) capitate (4) plumose
35. inflorescence shape at anthesis (0) hemispherical (1) ovate (2) obovate (3) obliquely ovate (4) linear-lanceolate (5) triangular (6) spherical (7) shapeless (8) linear (9) elliptical (10) cylindrical (11) lobed
36. pedicels and spikelets orientation relative to inflorescence axis (0) diverging from the inflorescence (1) parallel to inflorescence axis
37. inflorescence pedicels orienta (0) mostly erect (1) mostly patent
38. pedicels obscured or visible in inflorescence (0) obscured by the spikelets (1) not obscured by the spikelets
39. pedicels length relative to spikelet length (0) longer than the spikelets (1) as long as the spikelets (2) shorter than the spikelets (3) minute (4) absent
40*. pedicel indumentum (0) like the inflorescence branches (1) with a dense brush of hair at a node (2) with a brush of hair at the base of the spikelet (3) villous
41. inflorescence branches length relative to the spikelet length (0) longer than the spikelets (1) as long as the spikelets (2) shorter than the spikelets (3) minute
42. inflorescence branches indumentum (0) glabrous (1) scaberulous (2) puberulous (3) villous
43. inflorescence node indumentum, generally on the pulvinus (0) similar to pedicels (1) puberulous (2) villous
44. anther position at dehiscence (0) entangled in the stigmas (1) excerted from the florets
45. glume length relative to the cluster of florets (0) shorter than the cluster of florets (1) as long as the cluster of florets (2) longer than the cluster of florets
46. glumes length relative to basal lemma length (0) shorter than basal lemmas (1) as long as basal lemmas (2) longer than basal lemmas
47. glumes length relative to floret packet (0) twice as long as the florets (1) only slightly longer than the

florets
48. glumes with number of veins (0) 0 (1) 1 (2) 3 (3) 5 (4) 7 (5) 9 (6) 11 (7) 13
49. glumes central vein relative to lateral veins (0) not much better developed than the lateral veins (1) longer and much more prominent than the lateral veins
50. glumes margin texture (0) same as the body of the glumes (1) membranous
51. glume indumentum (0) hirsute (1) pubescent (2) glabrous (3) microscaberulous (4) scaberulous (5) puberulous (6) villous (7) tuberculate hairy
52. glume indumentum distribution (0) adaxial (1) basal (2) apical (3) middle (4) all over (5) along veins (6) along margins (7) along keels
53. callus width relative to inter (0) as wide as internode (1) wider than internode
54*. callus shape in adaxial view (0) acute (1) rounded (2) truncate
55. callus - internode junction in side view (0) horizontal (1) oblique
56. callus apex pungent or not (0) blunt (1) pungent
57. callus indumentum presence (0) glabrous (1) villous
58. callus indumentum organisation (0) in two tufts (1) disorganised (2) forming a velvety cover
59. callus indumentum length relative to lower group of lemma hairs (0) not reaching lemma hairs (1) as tall as lemma hairs (2) overtopping lemma hairs
60. second lemma texture (0) indurated or bony, hard in the fruiting stage (1) chartaceous or cartilaginous
61. second lemma back surface appearence (0) smooth, shiny (1) warty (2) smooth, dull (3) granular
62. second lemma veins anastomosing or not (0) anastomosing near apex (1) not anastomosing
63*. second lemma lateral margins straight or with auricles (0) straight (1) with auricles
64. second lemma apex shape (0) lobed (1) acute (2) truncate (3) lacerate (4) finely tridentate
65. second lemma apical shape if lemma acute (0) obtuse (1) acute (2) acuminate (3) long-acuminate (4) extended up the awn
66*. second lemma indumentum presce (0) pubescent (1) glabrous (2) scaberulous (3) puberulous (4) villous
67. second lemma indumentum distribution (0) scattered on back of lemma (1) aggregated into discrete tufts arranged in two transverse rows (2) in one or several submarginal tufts (3) as a long submarginal line of hairs, sometimes with scattered hair on back of lemma (4) tufted, but not in transverse lines (5) as a transverse row across the back
68. second lemma indumentum distribution if hairs are scattered (0) overall (1) basally (2) in the middle (3) along keel and margins (4) along veins (5) along margins (6) at the apex (7) in two tufts submarginal on lemma backs (8) in two vertical rows at the base of the lemma (9) between the veins
69. second lemma hairs distribution (0) more or less equal-sized over whole back (1) forming a large row below the sinus, smaller and sparser lower down (2) grading from short to long up the lemma back
70. second lemma upper hairs, if hairs are scattered, relative to the lemma lobes (0) obscuring the lemma lobes (1) about as long as the lemma lobes (2) significantly shorter than the lemma lobes
71. second lemma density of scattered hairs on the back of the lemma (0) sparse (1) moderate, so that lemma is still visible (2) dense, forming a felt
72. second lemma upper row of lemma hair tufts degree of development (0) complete (1) incomplete, with marginal and some dorsal tufts (2) incomplete, with only marginal tufts
73. second lemma lateral lemma lobes relative to upper row of lemma hairs (0) obscuring the lemma lobes (1) as long as the lemma lobes (2) shorter than the lemma lobes
74. second lemma lower row of hair tufts degree of completeness (0) complete (1) incomplete, with only marginal tufts (2) absent (3) incomplete, with marginal and some dorsal tufts (4) incomplete, with only dorsal tufts
75. second lemma length of the hair tufts relative to upper row (0) not reaching the upper row (1) as long as the upper row (2) longer than the upper row
76. second lemma indumentum between the hair tufts present of absent (0) glabrous (1) scattered hairs
77. organisation of indumentum on lemma back below upper row (0) scattered, without any pattern (1) in the center of the lemma back (2) in dense inter-nerve rows, long and dense, grading into the upper row of tufts (3) in dense, short internerve rows, abruptly distinct from the upper row
78. second lemma-lobes shape (0) truncate-lacerate (1) acute (2) acuminate (3) awned (4) rounded (5) obtuse
79. second lemma-lobes length relative to the lemma body (0) shorter than lemma body (1) as long as lemma body (2) longer than the lemma body, but not twice as long (3) twice as long as or more than lemma body
80. second lemma lobe texture (0) outer margins membranous (1) similar to rest of lemma (2) whole lobe membranous
81. second lemma-lobes indumentum (0) glabrous (1) scaberulous (2) puberulous (3) villous
82. second lemma-lobes indumentum (0) along margins only (1) on outer surface only (2) on inner surface only (3) on both surfaces
83. second lemma-lobes fusion to the awn (0) absent (1) for about half of the lobe len (2) for the full lobe length
84. second lemma lobe setae presen (0) present on lemma-lobes (1) absent from lemma-lobes
85. second lemma lobe setae length relative to lemma lobe length (0) distinctly shorter than lemma lobes (1)

about as long as the lemma lobes (2) distinctly longer than the lemma lobes
86. setae included or exerted from the glumes (0) included in the glumes (1) as tall as the glumes (2) exerted from the glumes
87. second lemma awn present or absent (0) present on the lemma (1) sometimes present on the lemma (2) absent from the lemma
88. awn length relative to setae (0) shorter than setae (1) as long as setae (2) longer than setae
89. awn differentiated into a column and limb (0) differentiated into a column and limb (1) of one part
90. awn geniculation (0) geniculate (1) straight
91. awn in cross-section (0) flat, forming a distinct column (1) round
92. awn straight or cork-screwed (0) straight (1) with one or two twists (2) twisted many times into a tight corkscrew
93. awn column length relative to lemma lobes and setae (0) shorter than lemma lobes (1) as long as lemma lobes (2) longer than lemma lobes but shorter than setae (3) as long as lemma lobe setae (4) longer than lemma lobe setae
94. palea shape: this refers to the region between the keels (0) elliptical to ovate (1) linear to lorate (2) obovate (3) oblong (4) subpandurate (5) spathulate
95. palea apex (0) acute (1) rounded (2) truncate (3) bilobed (4) awned (5) 3-lobed (6) obtuse
96. palea width relative to length (0) broad, 1-(3) times as long as wide (1) narrow, 3-(5) times as long as wide (2) linear, 5-(8) times as long as wide
97. palea length relative to awn knee (0) shorter than awn knee (1) as tall as awn knee (2) longer than awn knee
98. palea length relative to lemma (0) longer than the lemmas (1) as long as the lemmas (2) shorter than the lemmas
99. palea length relative to the lemma sinus (0) much longer than the lemma sinus (1) slightly longer than the lemma sinus (2) as long as the lemma sinus (3) shorter than lemma sinus
100. palea keels indumentum or ornamentation (0) glabrous (1) scabrid (2) ciliate (3) villous
101. palea body texture (0) chartaceous to cartilaginous (1) membranous (2) bony
102. palea indumentum between the keels (0) pubescent (1) absent (2) puberulous (3) villous
103. distribution of palea indumentum between the keels (0) all over (1) in lower half (2) in middle (3) in upper half
104. presence of tufts of long hairs on palea margin (0) absent (1) present
105*. palea margin indumentum in tufts or rows (0) as a single tuft either side (1) as a long row of hair
106. lodicules bristles presence (0) absent (1) present
107. density of lodicule bristles (0) very sparse, 1-(3) (1) sparse, 4-(5) (2) dense, more than (6)
108*. lodicules bristle length relative to lodicules length (0) as long as the lodicules (1) shorter than the lodicules
109. lodicule microhairs presence (0) present (1) absent
110. density of lodicule microhairs (0) sparse (1) moderate (2) dense
111. lodicule shape (0) square (1) obtriangular (2) cuneate and bilobed (3) hammer-shaped (4) rhomboid (5) spathulate (6) three-lobed, with central lobe longer than laterals
112. ovary apex central cleft presence (0) present (1) absent
113. caryopsis shape (0) lanceolate (1) lorate (2) ovate (3) elliptical (4) obovate (5) orbicular (6) turbinate
114. fruit a nut or caryopsis (0) a caryopsis (1) a nut (2) tardily separable
115. caryopsis colour (0) black (1) grey (2) dark brown (3) pale brown (4) yellow (5) reddish brown
116. caryopsis surface texture (0) shiny (1) dull and smooth (2) rugulose (3) colliculate (4) reticulate-foveolate (5) striate
117. caryopsis cross-sectional shape 1/3 from top (0) circular (1) plano-convex (2) concavo-convex (3) circular and grooved (4) elliptical (5) three-lobed
118. caryopsis cross-sectional shape 2/3 from top (0) circular (1) plano-convex (2) concavo-convex (3) circular and grooved (4) elliptical (5) three-lobed
119. caryopsis embryo mark width relative to caryopsis (0) narrower than caryopsis (1) as wide as caryopsis (2) wider than caryopsis
120. caryopsis embryo mark shape (0) oblong (1) circular (2) ovate (3) elliptical (4) obovate
121. caryopsis embryo mark length absolute (0) 1:10 of caryopsis length (1) 2:10 of caryopsis length (2) 3:10 of caryopsis length (3) 4:10 of caryopsis length (4) 5:10 of caryopsis length (5) 6:10 of caryopsis length (6) 7:10 of caryopsis length (7) 8:10 of caryopsis length (8) 9:10 of caryopsis length (9) 1 of caryopsis length
122. caryopsis hilum shape (0) linear (1) oblong (2) ovate (3) elliptical (4) obovate (5) punctiform
123. caryopsis hilum length as proportion of caryopsis length (0) 1:1(0) of caryopsis length (1) 2:1(0) of caryopsis length (2) 3:1(0) of caryopsis length (3) 4:1(0) of caryopsis length (4) 5:1(0) of caryopsis length (5) 6:1(0) of caryopsis length (6) 7:1(0) of caryopsis length (7) 8:1(0) of caryopsis length (8) 9:1(0) of caryopsis length (9) (1) of caryopsis length
124. apomictic reproduction presence and type (0) absent (1) present as apospory
125. leaf transectional anatomy type (0) mesic type (1) sclerophyllous type (2) intermediate type
126. leaf outline (0) expanded (1) setaceous
127. expanded, open blade, shape (0) V-shaped (1) U-shaped (2) inrolled margins (3) flat
128. setaceous, filiform, shape (0) V-shaped (lamina folded) (1) U-shaped (lamina rolled) (2) terete (3) tightly inrolled

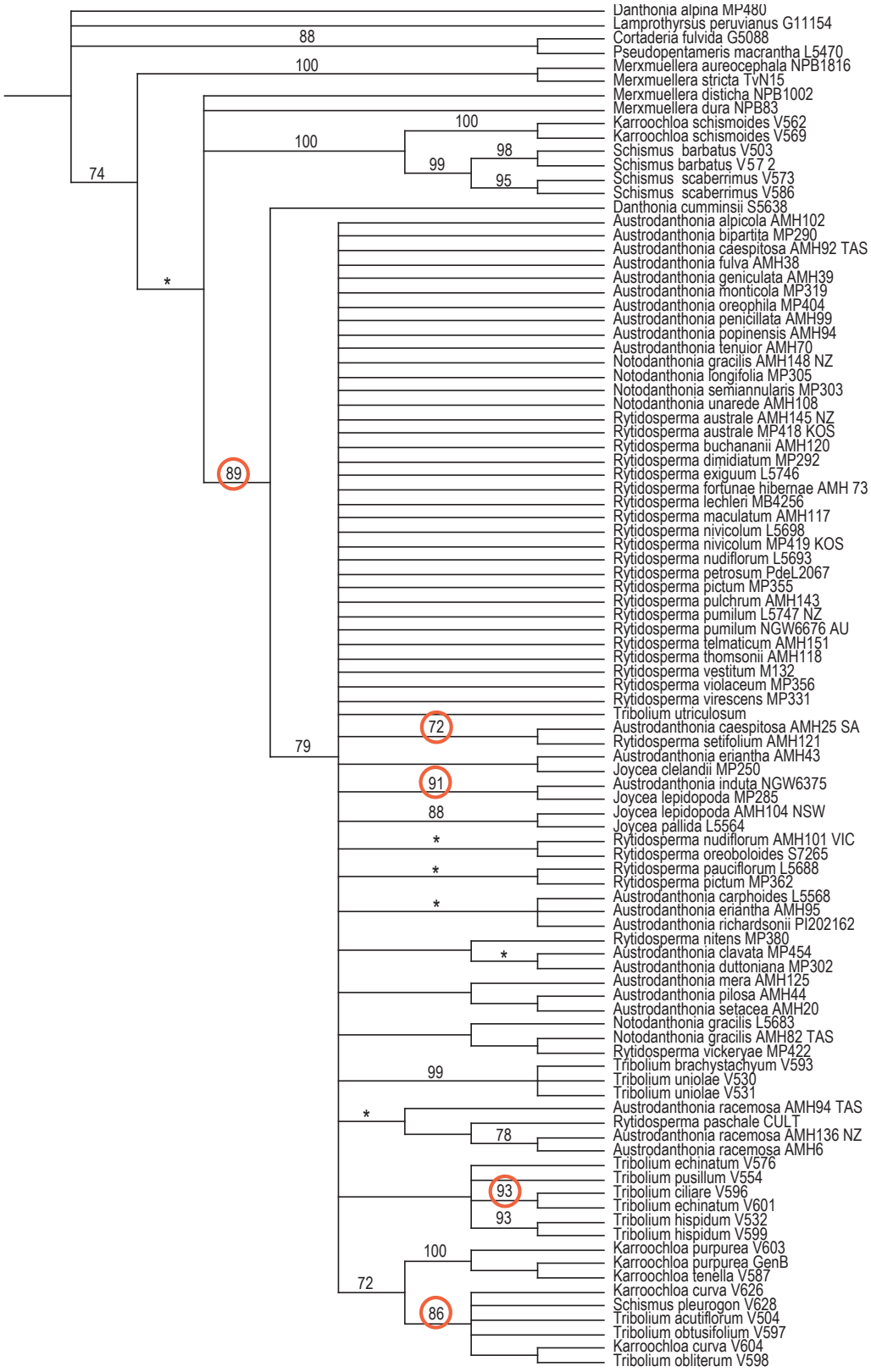
129. margin shape (0) gently tapering (1) abrupt and not tapering (2) thickened (3) a pointed projection
130*. presence of sclerenchyma cap on margin (0) with a sclerenchymatous cap (1) without a sclerenchymatous cap
131. width of marginal sclerenchyma cap (0) wider than costal zones, visible on leaf as a hyaline margin (1) narrower than costal zones, not forming a hyaline margin
132. adaxial ribs and furrows degree of development (0) absent (surface not ribbed) (1) slight (2) medium (3) massive with cleft-like furrow
133. furrows distribution relative to vbs (0) located between all vbs (1) located over three vbs (2) present either side of midrib only
134. furrow width relative to the ribs (0) as wide as ribs (1) 1/3-2/(3) width of ribs (2) less than 1/3 width of ribs, forming narrow clefts
135. apical shape of ribs (0) rounded (1) flat-topped (2) pointed
136. angle and curvature of rib sides (0) parallel (1) converging, straight (2) convex (3) diverging, straight (4) concave
137. rib size over 1'vbs and 3'vb (0) the same over 1'vbs and 3'vb (1) smaller over 3'vbs than 1'vb
138. presence of abaxial ribs and furrows (0) absent (1) present
139*. median vascular bundle degree of development (0) without midrib or parenchyma (same as lateral vb) (1) forming a keel and associated with colourless parenchyma (2) forming a midrib but with no associated parenchyma
140. position of vbs in leaf blade (0) all vbs situated in centre of (1) all vbs closer to abaxial surf (2) all vbs closer to adaxial surf (3) vbs of different orders at dif
141. smaller bundles differentiated into 2' and 3' vbs or not (0) differentiated into 2'vbs and 3'vbs (1) all the same
142. distribution of 3'vbs relative to 1'vbs (0) between all 1'vbs (1) only between midrib and first pair of 1'vbs (2) between midrib and first two pair of 1'vbs (3) between most 1'vbs
143*. sclerenchyma girders and strands distribution relative to 1'vbs and 3'vbs (0) with all vbs (1) only with 1'vbs
144. 1'vbs outline shape (0) circular (1) elliptical
145. 1'vbs phloem presence of thickened (0) with a sheath of lignified cells (1) without lignified cells or with only the ibs lignified
146. 1'vbs metaxylem vessels diameter (0) narrow (1) of medium diameter (2) wide
147. 1'vbs outer bundle sheath interruption (0) entire (1) with adaxial interruptions only (2) with abaxial interruptions only (3) with adaxial and abaxial inter ruptions
148. outer bundle sheath cells in 1'vbs conspicuous or not (0) inconspicuous (1) conspicuous (2) smaller than chlorenchyma cells
149. 1'vbs bundle sheath extension (0) absent (1) present
150. 1'vbs inner bundle sheath walls thickening (0) thickened anticlinally (1) not thickened (2) thickened all round
151. ibs of 1'vbs cell size relative to obs cells (0) smaller than obs cells (1) the same size as the obs cells (2) larger than the obs cells
152. 1'vbs adaxial sclerenchyma development and shape (0) as small strands (1) as small girders (2) as girders narrowing towards vbs (3) as T-shaped girders or inversely anchor-shaped girders (4) absent
153. 1'vbs abaxial sclerenchyma development and shape (0) small strands (1) narrow girders (2) shallow girders (3) trapezoidal girders (4) massive linked girders, forming a continuous subepidermal layer (5) continuous subepidermal layer not linked to vbs
154. 3'vbs outer bundle sheath interruptions (0) entire (1) with adaxial interruption only (2) with abaxial interruption only (3) with adaxial and abaxial interruptions
155. 3'vbs outer bundle sheaths co (0) inconspicuous (1) conspicuous (2) smaller than chlorenchyma cell
156. 3'vbs bundle sheath extension (0) absent (1) present
157. 3'vbs ibs cells size relative to obs cells (0) smaller than obs cells (1) the same size as the obs cells (2) larger than the obs cells
158. 3'vbs inner bundle sheath walls thickening (0) thickened anticlinally (1) not thickened (2) thickened all round
159. 3'vbs adaxial sclerenchyma degree of development and shape (0) as small strands (1) as small girders (2) as girders narrowing towards v (3) as T-shaped girders or inverse (4) absent
160. 3'vbs abaxial sclerenchyma degree of development and shape (0) as small strands (1) as narrow girders (2) as shallow girders (3) as trapezoidal girders (4) as massive linked girders, forming a continuous subepidermal layer (5) as a continuous subepidermal layer not linked to vbs (6) absent
161. 3'vbs phloem presence of thickened sheath (0) with a sheath of lignified cells (1) without lignified cells or with only the ibs lignified
162. mesophyll intercellular spaces (0) diffuse parenchymatous chlorenchyma with intercellular air spaces (1) large angular parenchymatous chlorenchyma with intercellular air spaces (2) small, angular isodiametric chlorenchyma cells with small air spaces
163. abaxial epidermal cell size relative to adaxial cells (0) all larger than adaxial ones (1) of intercostal zones only larger than adaxial ones (2) similar in size to adaxial epidermal cells
164. abaxial epidermis cuticle thickness (0) outer wall equal inner wall (1) outer wall twice as thick as inner wall (2) outer wall more than twice as thick as inner wall

165. abaxial epidermis wall thickness (0) wall equal to mesophyll walls (1) wall thicker than mesophyll walls
166. adaxial epidermis outer wall thicker than inner wall (0) without a thickened cuticle (1) with a much thickened outer wall
167. adaxial epidermis presence of bulliform cells in 2+ furrows (0) absent (1) present
168. adaxial epidermis presence of (0) present (1) absent
169. secondary walls of girder cell (0) lignified (1) cellulose
170. abaxial epidermal zonation presence (0) present (1) absent
171. intercostal long cells shape (0) rectangular (1) hexagonal (2) inflated
172. intercostal long cell, wall thickness (0) walls unthickened (1) walls slightly thickened (2) walls moderately thickened (3) walls heavily thickened (4) walls pitted
173. intercostal long cell wall undulations (0) straight (1) slightly undulating (2) moderately sinuous (3) deeply sinuous
174. intercostal short cell presence and distribution in long cells files (0) absent (1) long cells separated by single short cells (2) long cells separated by pairs of short cells (3) long cells separated by cork-silica cell pairs (4) long cells separated by single silica bodies (5) long cells separated by hooks
175. costal long cell, wall thickness (0) walls unthickened (1) walls slightly thickened (2) walls moderately thickened (3) walls heavily thickened (4) walls pitted
176. costal long cell, wall undulations (0) straight (1) slightly undulating (2) moderately sinuous (3) deeply sinuous
177. costal associated cells in long cell files (0) without short cells (1) separated by single short cell (2) separated by pairs of short cells (3) separated by cork-silica cell pairs (4) separated by single silica bodies (5) separated by hooks
178. costal long cells, shape relative to the intercostals long cells (0) larger in all dimensions than intercostals long cells (1) about the same size as intercostals long cells (2) smaller in all dimensions than intercostals long cells
179. stomata presence and shape (0) absent (1) low dome-shaped (2) high dome-shaped (3) tending to parallel sided type (4) triangular
180. stomata presence or with papillae (0) absent (1) flush with the epidermis (2) overarched by inflated papillae
181. stomatal files separated by how many long cells (0) separated by more than one file of long cells (1) separated by one file of long cells (2) adjoin one another
182*. abaxial prickle presence and shape (0) absent (1) costal, with short barbs (2) intercostal, small, with long barbs
183. abaxial, intercostal microhairs presence (0) present (1) absent
184. abaxial microhair relationship between basal and distal cells (0) with basal and distal cells of equal length (1) with basal cell slightly longer than the distal cell (2) with the basal cell much longer than the distal cell (3) with the basal cell shorter than the distal cell
185. abaxial intercostal macrohairs presence and type (0) stiff with thick walls (1) soft with thin walls (2) absent
186. abaxial intercostal macrohair type (0) bulbous (1) constricted (2) undifferentiated
187*. abaxial intercostal macrohairs base (0) associated with a raised cushion (1) associated with a few raised epidermal cells (2) not associated with specialized epidermal cells
188*. abaxial multicellular glands description (0) absent (1) stalked with a bulbous head (2) crateriform, unstalked (3) sunken below the level of the epidermis (4) sessile and linear
189. abaxial intercostal silica bodies description (0) absent (1) tall and narrow (2) round, single (3) round, enfolded by cork cell (4) kidney shaped (5) irregularly dumbell-shaped (6) angular dumbell-shaped (7) elongated dumbell-shaped (8) elongated, nodular (9) saddle-shaped 10 cross-shaped
190. abaxial costal silica bodies description (0) absent (1) tall and narrow (2) round, single (3) round, enfolded by cork cell (4) kidney shaped (5) irregularly dumbell-shaped (6) angular dumbell-shaped (7) elongated dumbell-shaped (8) elongated, nodular (9) saddle-shaped
191. adaxial papillae presence and type (0) absent (1) small, cuticular (2) inflated
192*. adaxial papillae shape (0) rounded (1) lobed (2) clavate (3) pointed and at end of cell
193*. adaxial papillae distribution (0) on the flanks of the ribs (1) on the crowns of the ribs
194. adaxial prickle hairs presence (0) absent (1) with short barbs (2) with long barbs, macrohair-like
195. adaxial prickle distribution (0) all over surface (1) only on the ribs (2) only in furrows
196. adaxial microhairs presence and apical to basal cell ratios (0) absent (1) with distal and basal cells equal in length (2) with distal cell longer than basal cell (3) with distal cell shorter than basal cell (4) with very short distal cell, elongate (5) present
197. adaxial microhairs distribution (0) scattered on surface (1) restricted to furrows (2) along the base of the ridges next to bulliform cells
198*. adaxial microhairs density (0) dense, overlapping (1) sparse, not overlapping
199. adaxial macrohairs presence and description (0) absent (1) stiff with distinct raised cushion (2) flexible with few specialized epidermal cells associated with the base
200. glume colour (0) green with purple (1) green (2) straw, pale green (3) purple, yellow/brown (4) green (-purple) - red
201. upper glume differs from lower glume in (0) nothing (1) number veins (2) size (3) shape (4) hairiness
202. anther colour (0) yellow (1) white (2) orange - yellow (3) red - purple
203. diploid chromosome number recorded (0) 12 (1) 24 (2) 48 (3) 36 (4) 72 (5) 56 (6) 20

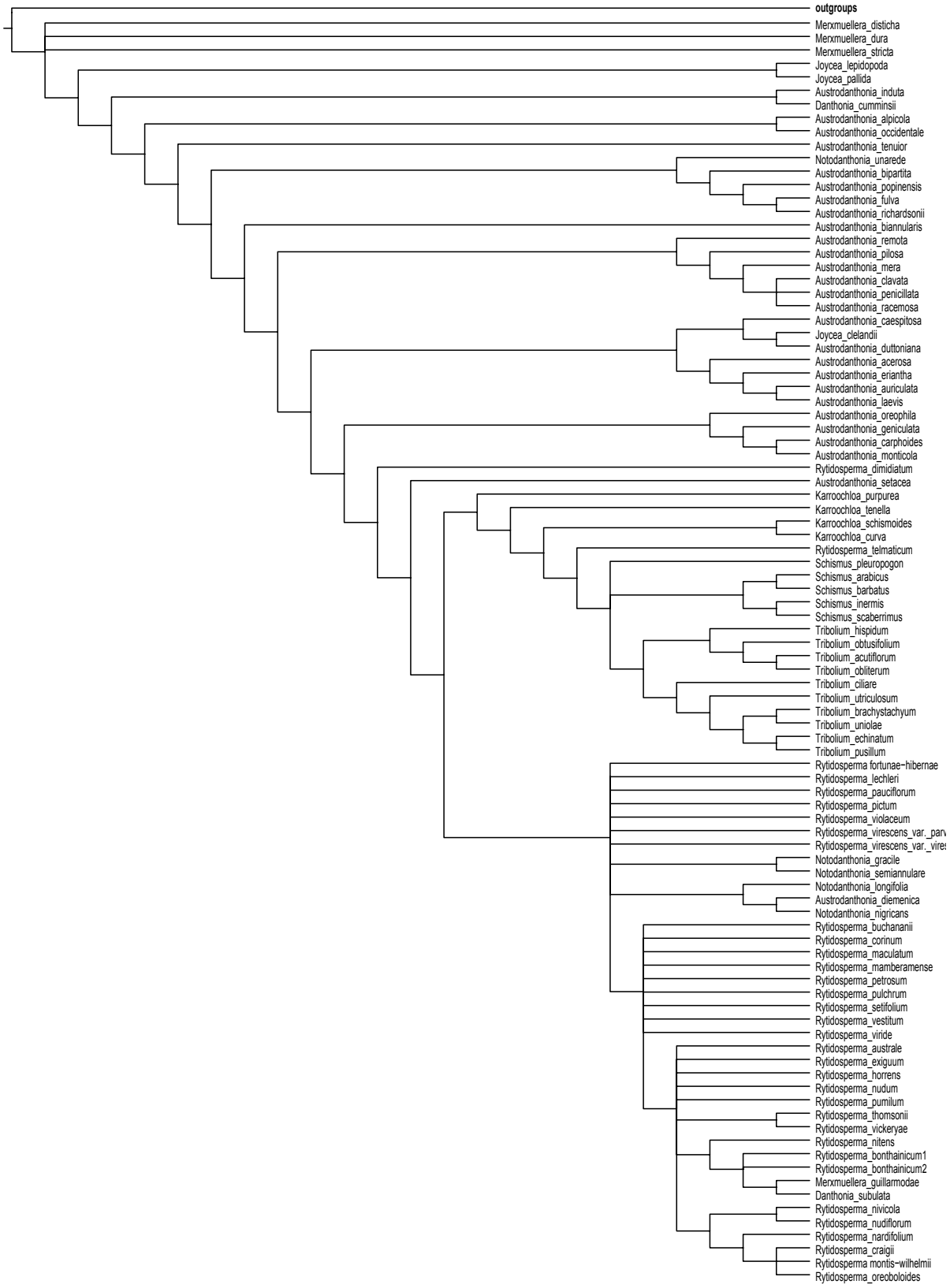
204. chromosome complements (0) 2 (1) 4 (2) 6 (3) 8 (4) >12
205*. tussock diameter at base (0) 1-50 (1) >50
206. tussock diameter - table height (0) <200 (1) >200
207. tussock height (0) <0.5 (1) >0.5
208. leaf table height (0) <100 (1) 100-200 (2) >200
209. height of inflorescence (0) <300 (1) >300
210. Inflorescence length (0) <1 (1) 1.5-3.0 (2) >4.0
211. culms nodes (0) one (1) two (2) three (3) >three
212. ligule length (0) <0.4 (1) 0.5-1 (2) >1
213. leaf blades length (0) <150 (1) 151-300 (2) >300
214. leaf blades width (0) <1.0 (1) 1-2 (2) >2
215. spikelets/inflorescence (0) <20 (1) 20-100 (2) >100
216. inflorescence length (0) <50 (1) >50
217. inflorescence width (0) <20 (1) >20
218. female fertile spikelet length (0) <5 (1) 5-12 (2) >12
219. number florets/spikelet (0) 1-5 (1) >5
220. glumes length (0) <5 (1) 5-15 (2) >15
221. number glume veins (0) <5 (1) >5
222. glume width (0) <2.5 (1) >2.5
223. callus length (0) <0.4 (1) 0.5-1.0 (2) >1.0
224. rachilla internode length (0) <0.5 (1) 0.5-1.0 (2) >1.0
225. callus:callus+rachilla (0) <0.5 (1) >0.5
226. second lemma length (0) <3.5 (1) 3.5-5.5 (2) 6.0)
227. second lemma veins (0) >(9) (1) (9)
228. second lemma upper hairtufts length (0) >2 (1) 2.5-4.0 (2) >4.5
229. second lemma distance sinus - upper hairs (0) <0.4 (1) 0.5-1.0 (2) >1.0
230. second lemma length lower hairtufts (0) <0.5 (1) 0.5-2.0 (2) 2.0
231. second lemma lobes length (0) <2.2 (1) >2.4
232. second lemma number veins in lobes (0) one (1) two (2) three
233. second lemma setae length (0) <1 (1) 1.3-3.7 (2) >4
234. second lemma setae + lobes length (0) >0.8 (1) 0.9-5.8 (2) >5.9
235. second lemma awn length (0) <3.2 (1) 4-12 (2) >12.5
236. second lemma column length (0) <3.5 (1) >4.0
237. second lemma limb length (0) <(7) (1) >(7)
238. second lemma palea length (0) <(5) (1) 5-10 (2) >10
239. second lemma palea width (0) <1 (1) 1-2 (2) >2
240. number lodicule veins (0) <3 (1) 3 (2) >3
241. anther length (0) <2.3 (1) >2.5
242. caryopsis length (0) <1 (1) 1-2.5 (2) >2.5
243*. caryopsis width (0) <2 (1) >2
244. embryo mark length (0) <0.5 (1) 0.5-1 (2) >1
245. embryo length:tot caryopsis length (0) <0.34 (1) 0.4-0.6 (2) >0.7
246. Hilum length (0) <1 (1) >1.5
247. hilum length:tot caryopsis length (0) <0.33 (1) >0.5
248. number l'vbs in leaf section (0) one (1) 2 or 3 (2) >3
249. number smaller bundles between l'vbs (0) one (1) two or three (2) >3

*uninformative characters

Electronic Appendix I. Strict consensus tree of analysis of *ITS* data. Nodes in conflict (≥ 70% BS) with the cpDNA tree are marked in red.



Electronic Appendix II. Morphological cladogram based on analysis of equally weighted (EW) character matrix.



Chapter 3.

ECOLOGY AND EVOLUTION OF THE DIASPORE 'BURIAL SYNDROME'

A.M. Humphreys, A. Antonelli, M.D. Pirie and H.P. Linder

Evolution (submitted)

Abstract

Hygroscopically active awns or 'bristles' have long intrigued scientists. Experimental evidence shows that they are important for diaspore burial in the correct orientation, thereby increasing successful seed germination and seedling survival. Despite these ecological advantages, 38 of the 280 species of grasses in Danthonioideae lack awns. The awnless state has arisen ca. 25 times independently and we provide the first evidence that the ecological disadvantage of not having an awn also applies in an evolutionary context. Awnless clades generally contain fewer species than their awned sisters and awn loss has occurred significantly more recently than expected by chance, suggesting that lineages in which awn loss occurs diversify little and do not persist. Awnless ancestors have diversified to form a clade of primarily awnless descendents only in genera *Tribolium* and *Schismus*. Several species in these genera are annual and we find a significant correlation between the evolution awns and the evolution of life history. A suite of other diaspore traits accompany the awned or awnless states. We interpret the awn as being the visible constituent of a compound 'burial syndrome', the two ecological extremes of which may explain the correlation between awns and life history and provides an explanation why awnless species in *Tribolium* and *Schismus* persist.

Introduction

A major goal of macroevolutionary studies is explaining imbalances in the distribution of biodiversity among clades in the tree of life. One established route through this endeavour is to test the possible role of intrinsic factors (traits, 'key innovations' (Miller 1949)) in generating greater species richness in the group that possesses such an innovation, compared to its sister group (Mitter et al. 1988; Barraclough et al. 1995; Hodges and Arnold 1995) or increases in diversification rates (Sanderson and Donoghue 1994; Klak et al. 2004; Moore and Donoghue 2007, 2009) beyond that expected by chance (Slowinski and Guyer 1989a, b). Classic examples of biological traits that are associated with increased species richness include nectar spur length in *Aquilegia* (Hodges and Arnold 1995; Ree 2005), sexual selection by female choice in birds (Barraclough et al. 1995; Mitra et al. 1996) and phytophagy in insects (Mitter et al. 1988). The idea behind each of these cases is that if the presumed key innovation evolves in a suitable ecological setting (Miller 1949; de Queiroz 2002) it will allow entrance to novel adaptive space, promote diversification and thereby generate imbalances in diversity among clades.

What, then, might the consequences of losing such innovations be? The evolution of photosynthesis in free-living cyanobacteria and their subsequent endosymbiosis with non-photosynthesising bacteria opened up completely novel trophic space and is one of the innovations that have led to the evolution of the plant kingdom (Niklas 1997; Leslie 2009). Photosynthetic activity provides the carbon source that is necessary for all plant life and is such a sophisticated innovation that it is unlikely to be lost. However, the ability to photosynthesise has been lost in several lineages of flowering plants, at least eight times independently (Kujit 1969; Barkman et al. 2007). Such losses would be highly detrimental were it not for the ecological shift to a holoparasitic life style that preceded these losses (Kujit 1969). Another trait that may seem equally unlikely to be lost is the ability to fly. Powered flight has been proposed as a key innovation in both birds and insects (Roff 1994) because it confers a range of advantages including increased possibility to escape predators and expand foraging space. Despite this, loss of flight has occurred numerous times in both birds (Roff 1994; Harshman et al. 2008) and insects (Wagner and Liebherr 1992; Whiting et al. 2003), each time the ecological advantage of the ability to fly no longer outweighs the energetic costs of its maintenance (e.g. McNab 1994).

Losses of key innovations have thus clearly occurred repeatedly, without necessarily conferring a detrimental effect on diversification, as might be expected based on the increased opportunities for diversification offered by the acquisition of such traits. Here we hypothesise that such 'successful' losses of innovations can only have occurred after, or simultaneously with, 1) the occurrence of an ecological shift that has turned an otherwise deleterious shift to an advantage and 2) a suite of morphological and/or physiological changes that have reinforced the selective advantage of the new state. We investigate this hypothesis in grasses that have lost their awn ('bristle'), a structure known to be important during seed dispersal, in particular for promoting successful burial and establishment.

Many plant species have structures that increase efficiency of seed dispersal, e.g. hooks and spines for catching on to fur in chestnut (*Castanea*), sail-like structures for capturing the wind in sycamore (*Acer*) or structures that coil and uncoil in response to changes in air humidity and thereby propel seeds across a soil surface or drill seeds firmly into the ground in geraniums (*Erodium*). In grasses (Poaceae) this hygroscopic activity is exhibited by awns attached to the diaspore. We use 'diaspore' to describe the dispersal units in grasses consisting of a one-seeded nut (caryopsis or achene) in which the ovary wall is usually fused with the seed coat, together with the "chaff", the lemma and the palea (Fig. 1). Early accounts of hygroscopic activity of grass awns focussed on describing the mechanics of the torsion activity (e.g. Hildebrand 1873; Zimmerman 1879; Murbach 1900). Later studies demonstrated that

this activity caused movement of diaspores in petri dishes upon wetting and drying (Simpson 1952) and suggested that their role in seed (or diaspore) dispersal was primarily in burial (Stebbins 1971, 1974). Peart (1979, 1981, 1984) showed that the depth and orientation of burial significantly influences percentage germination, that the presence of a hygroscopically active awn dramatically increases the proportion of seed lodged in suitable microsites in the soil, that removal of increasing portions of the awn decreases the percentage of seed that germinates and that the presence of the awn affects soil type preferences, both under experimental and field conditions. Together with more recent studies on both ecological and mechanical aspects of hygroscopically active awns (Garnier and Dajoz 2001; Elbaum 2007; Kulic et al. 2009) these studies have firmly established that having a well developed awn provides an ecological advantage, enhancing seed dispersal, burial, germination and establishment. Accordingly, we expect species that have lost their awn to be at a selective disadvantage compared to their awned competitors.

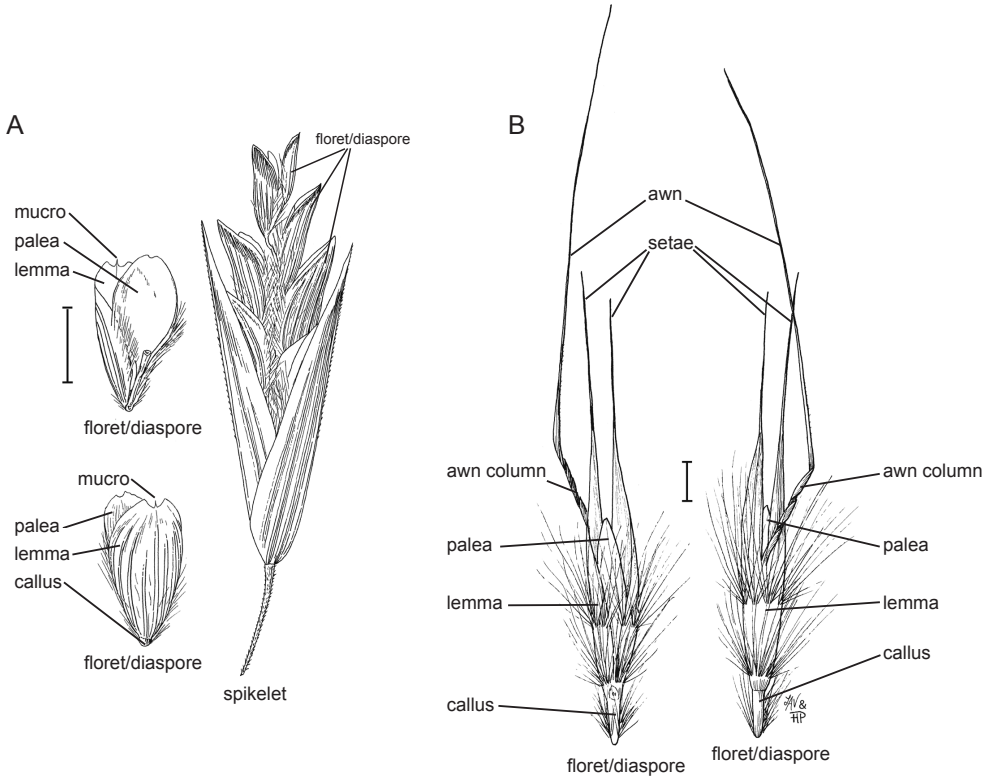


Figure 1. Diaspores that constitute two extremes of the burial syndrome. The floret encompasses the lemma and the palea that together enclose the male and female parts. After fertilisation, seed maturation takes place between the lemma and palea, in the caryopsis [or achene; not visible in this figure], and together the lemma, palea and caryopsis (or achene) constitute what we refer to as the diaspore. Modified from Barkworth et al. (2007) with permission. Copyright is owned by Utah State University Press and the original illustrations were drawn by Linda A. Vorobik and Hana Pazdírková. Scale bar = 1 mm. **A.** *Schismus barbatus.* Top floret/diaspore, dorsal view. Bottom floret/diaspore, ventral view. Note that the lemma lacks an awn but instead terminates in a mucro, has a short, glabrous callus and lemma indumentum only at the lemma margins. We postulate that this character combination leads to a diaspore that is optimised for passive burial. **B.** *Rytidosperma caespitosa.* Left floret/diaspore, dorsal view. Right floret/diaspore, ventral view. Note the deeply lobed lemma, terminating in two lateral setae, with a well developed awn inserted at the lemma sinus. The twisted awn column is the result of hygroscopic activity. Note also the densely indumentous lemma back and the long, hairy callus. This character combination leads to a diaspore that is optimised for active burial in the correct orientation.

Typically the species of the Danthonioideae (Barker et al. 2001), one of the smaller grass subfamilies, have a conspicuous, hygroscopically active awn, borne in a sinus on the lemma (Fig. 1B). But, remarkably, 38 out of the 280 species of danthonioid grasses have awnless diaspores (Fig. 1A). Awnless species are distributed on several continents and among numerous genera: in Africa (*Pentameris, Schismus*, *Tribolium*), in South America (*Cortaderia*) and in Australasia (*Notochloe* and *Rytidosperma*). Recent molecular phylogenetic analyses (Barker et al. 2003; Verboom 2006; Galley and Linder 2007; Pirie et al. 2008; Humphreys et al. 2010) have provided a robust phylogenetic framework within which further evolutionary study can be based and which has also enabled a reconsideration of generic limits in a phylogenetic context (Linder et al. accepted manuscript). This has the practical advantage that each of the major clades corresponds to a genus and can thus be referred to by its generic name. We use this phylogenetic framework to analyse the evolution of the awns and to test whether the disadvantage of not having an awn in an ecological context, holds true also in an evolutionary context, in terms of lineage persistence and diversification. We also quantify variation in other diaspore traits that may be linked with the awned versus the awnless state to test if awnless species may have undergone further morphological changes following awn loss. We show that awns have been lost several times independently and that most of these loss events are associated with reduced species diversity. We also show that the awn is the conspicuous constituent of a compound 'burial syndrome' and that the evolution of awns is correlated with life history evolution, suggesting that the awnless state is maintained if it is accompanied by an ecological shift to passive burial and into habitats where hygroscopically active awns offer little advantage.

Materials and Methods

Taxon sampling, molecular markers and phylogeny reconstruction

We based the phylogenetic reconstruction on a modified version of the combined chloroplast DNA (cpDNA) and nuclear ribosomal DNA (nrDNA) supermatrix for the Danthonioideae generated by Pirie et al. (2008). *Rytidosperma acerosum*, *R. occidentalis* and *R. petrosum* were added to the matrix and *R. vestitum* and *R. fortunae-hibernae* were removed, due to their positional instability among trees found in previous analyses (Humphreys et al. 2010). Taxon sampling was thus brought to 81% overall (for taxon sampling per clade (=genus) see Table 1). Non-coding markers trnT-L and trnC-ycf6-psbM-trnD, as well as the protein coding ndhF marker, were added for most *Rytidosperma* species and coding regions rbcL and matK were added to 21 and 28 placeholder taxa, respectively, following the strategy of Pirie et al. (2008). All newly added data were generated by Humphreys et al. (2010) and were included here to improve resolution in *Rytidosperma*. Sequences were added to the existing data matrix and aligned manually, since no regions of ambiguous alignment were encountered. Taxa for which no new data were added were scored as unknown '?'. Gaps were coded as missing data '—'. The final aligned matrix comprised 299 taxa and 14,425 characters.

The best-fitting evolutionary model for the data set was chosen using ModelTest (Posada and Crandall 1998). To overcome some of the computational difficulties in analysing such a large data set in a Bayesian framework (Pirie et al. 2008), we performed the phylogenetic analysis in two steps. First, a Maximum Likelihood analysis was run in the software GARLI 0.960 (Zwickl 2006), with seven independent runs under the GTR+Γ+I model and with stepwise sequence addition and no outgroup rooting. All runs were performed in the CIPRES cluster at the San Diego Supercomputer Center (http://www.phylo.org/portal2). Second, the most likely tree obtained in the GARLI analysis was used as a starting tree for phylogenetic

inference in a Bayesian framework. Six independent runs of 1.2 x 10^6 generations each were performed in MrBayes v. 3.1 (Huelsenbeck and Ronquist 2001), using four chains (1 cold and 3 heated), sampling every 500th generation and saving branch lengths. Three different temperatures were applied for the heated chains in three sets of parallel runs: 0.1, 0.2 and 0.3. All analyses were performed at the Computational Biology Service Unit hosted by Cornell University, USA (http://cbsuapps.tc.cornell.edu). Performance was evaluated using Tracer v.1.4.1 (Rambaut and Drummond 2007) and AWTY (Nylander et al. 2008) and convergence was considered to have been reached when effective sample size values of the combined runs were >100 and posterior probabilities (p.p.) for nodes remained stable among generations. Node posterior probabilities were calculated on 11,406 trees, after 3,000 trees were discarded as burn-in.

Gene tree conflict can have an impact on phylogeny based evolutionary inference (Pirie et al. 2009). Twenty seven accessions for which the phylogenetic position inferred by cpDNA is significantly different from that inferred by nrDNA were therefore represented by the individual genomes separately, using the taxon duplication technique of Pirie et al. (2008; 2009). In addition, multiple accessions of taxa can influence the proportions of terminals coded for particular states (such as awns present versus absent), which could result in a bias in character optimisations equivalent to changing the base frequencies in a nucleotide substitution model. Multiple accessions of species that are not demonstrably polyphyletic were therefore reduced to a single accession. This was achieved by pruning taxa from a random subset of 1,000 post-burnin Bayesian trees in Paup* 4.0b10 (Swofford 2002) whilst retaining the original branch lengths: Seventeen accessions were thus removed and accessions with disparate positions were kept for two taxa: *Pentameris pallida* and *Rytidosperma caespitosum*. In addition, a taxon of uncertain identity was kept: *Rytidosperma* sp. (accession AMH104). Thus, a set of 1,000 randomly sampled post-burnin phylograms, comprising 274 accessions, representing 228 species and including six outgroup taxa was created. This forms the phylogenetic framework in which the following analyses were carried out.

Morphological data and character coding

Information on the lemma awn, lemma indumentum, callus indumentum, callus length and life history (see below) was exported from our DELTA database (Linder et al. in prep) and gaps were filled using floras and species accounts (Conert 1965; Conert and Türpe 1969, 1974; Davidse 1988; Linder and Ellis 1990; Barker and Ellis 1991; Barker 1993, 1995; Baeza 1996; Laegaard 1997; Linder and Davidse 1997; Verboom and Linder 1998; Barker 1999; Edgar and Connor 2000; Baeza 2002; Darbyshire 2003; Linder 2004; Molloy and Connor 2005; Galley and Linder 2006; Clayton 2006 (onwards)). Each variable was coded as a binary character (Table 1), except callus length, for which raw measurements were used (see below). Coding/length for each species is listed in Appendix I.

Table 1. Character coding and percentage sampling per state (not counting duplicated taxa). Awns were coded as present (0) or absent (1). Absence of an awn denotes species in which the awn is altogether absent or reduced to a 'mucro', i.e. reduced beyond hygroscopic function. Callus and lemma indumentum were coded as villous (0) or glabrous (1), with 'glabrous' coded only for those species that never produce hairs on these surfaces. Polymorphic species were coded as (0). Sampling per clade is not relevant for these characters because these data were not analysed in a phylogenetic framework. Life history was coded as perennial (0) or annual (1). Four species of *Pentameris* are biannual (Linder and Ellis 1990) and these were coded as perennial to distinguish species that survive as adult plants for more than one growing season from those that do not.

Genus (clade)	Taxon sampling	Awned (0)	Awned sampled	Awnless (1)	Awnless sampled	Perennial (0)	Perennial sampled	Annual (1)	Annual sampled
Austroderia	100%	5	100%	0	n/a	5	100%	0	n/a
Capeochloa	100%	3	100%	0	n/a	3	100%	0	n/a
Chaetobromus	100%	1	100%	0	n/a	1	100%	0	n/a
Chimaerochloa	100%	1	100%	0	n/a	1	100%	0	n/a
Chionochloa	92%	25	92%	0	n/a	25	92%	0	n/a
Cortaderia	68%	16	75%	3	33%	19	68%	0	n/a
Danthonia	60%	24	58%	1	100%	25	60%	0	n/a
Geochloa	100%	3	100%	0	n/a	3	100%	0	n/a
Merxmuellera	57%	7	57%	0	n/a	7	57%	0	n/a
Notochloe	100%	0	n/a	1	100%	1	100%	0	n/a
Pentameris	90%	71	89%	13	100%	76	89%	8	100%
Plinthanthesis	100%	1	100%	2	100%	3	100%	0	n/a
Pseudopentameris	100%	3	100%	0	n/a	3	100%	0	n/a
Rytidosperma	74%	68	72%	5	100%	73	74%	0	n/a
Schismus	80%	1	100%	4	75%	2	50%	3	100%
Tenaxia	75%	8	75%	0	n/a	8	75%	0	n/a
Tribolium	93%	5	80%	9	100%	9	89%	5	100%
Danthonioideae	81%	242	80%	38	92%	264	80%	16	100%

Reconstructing the evolution of awns in Danthonioideae

Models of evolutionary change in morphological characters may make use of branching pattern alone or may include branch length information. Branch lengths may be in units of genetic divergence or time. Evidence for a correlation between rates of molecular change and rates of morphological change is contradictory (Omland 1997; Bromham et al. 2002; Davies and Savolainen 2006; Xiang et al. 2008) and under certain situations, e.g. rapid radiations or selective sweeps (Cunningham 1999), neither time nor genetic divergence (of most markers) is likely to be an accurate predictor of phenotypic change. In fact, generation time may provide a more realistic approximation of phenotypic change (Pagel 1999; Smith and Donoghue 2008; Smith and Beaulieu 2009). This is clearly an area demanding further attention, but the limited empirical evidence that is available suggests that neither genetic divergence nor time is expected to be a superior predictor of morphological change (Moore and Donoghue 2007; Smith and Beaulieu 2009). We used the set of 1,000 phylograms described above to analyse the evolution of awns for pragmatic reasons: to avoid zero-length branches or having to make transformations of branch lengths. Character evolution was reconstructed with (Maximum Likelihood [ML], reversible-jump MCMC [rj-mcmc]) and without (parsimony) the use of branch length information.

Parsimony reconstruction of awn presence at each node was implemented using the Trace Character Over Trees command in Mesquite v. 2.71 (Maddison and Maddison 2009). States were summarised for each node by counting all trees with uniquely best states. If no state is more parsimonious than the other the reconstruction at that node will be equivocal. We tested for phylogenetic constraint in awn evolution by permuting the terminals 1,000 times using the Reshuffle Terminal

Taxa command. This allowed numbers of inferred gains and losses required on the observed trees to be compared to a null distribution of gains and losses.

A problem with summarising ancestral states at individual nodes across a large sample of trees is that phylogenetic uncertainty can be confused with uncertainty in the ancestral state reconstruction. The 'most recent common ancestor' (mrca) approach of Pagel et al. (2004) provides a means for combining both sources of uncertainty. Nodes of interest are defined as the mrca of a given set of taxa (Pagel et al. 2004). Where a phylogenetic hypothesis has low support, the mrca of a set of taxa will be variable across trees. If the likely ancestral state is sensitive to this variation, support for the reconstruction will be correspondingly low, limiting what useful inferences can be made about the reconstructed ancestral state. If the likely ancestral state is not sensitive to this variation, then the reconstruction may be robust irrespective of node support. To minimise the influence of phylogenetic uncertainty on posterior support for ancestral state reconstruction we defined nodes of interest primarily as those with p.p. ≥ 0.80. In three cases we defined less conservative nodes: 1) mrca of *P. reflexa* and *P. ecklonii* (average diversity across 1,000 trees: [ñ]=9.54), 2) mrca of *N. microdon* and *C. jubata* [ITS] (ñ=13.7) and 3) mrca of *R. exiguum* and *R. oreoboloides* (ñ=10.9). In some trees these nodes are identical to more robust, more inclusive nodes and thus redundant. In other trees these nodes may provide additional information about awn loss events towards the tips of the phylogeny. We did not define nodes in clades that are invariable for the awn character, e.g. *Chionochloa*, where all species have an awn. In total 93 nodes were defined.

Determination of rate parameters and the most suitable model of evolution was carried out with 1×10^6 iterations of ML analysis using the Multistate commands in BayesTraits (available from http://www.evolution.rdg.ac.uk/BayesTraits.html). Best fitting models were identified using a likelihood ratio (LR) test (Edwards 1972). In this approach states at individual nodes are reconstructed as the state that maximizes the probability of arriving at the observed states in the terminals, given the model of evolution and the sample of trees (allowing the states at all other nodes to vary; Schluter et al. 1997; Pagel 1999). Ancestral state reconstruction in a Bayesian framework with rj-mcmc (Pagel and Meade 2006) was performed using the BayesMultistate (Pagel et al. 2004) commands in BayesTraits. This approach has the advantage that all possible models of evolution are sampled in proportion to their posterior probabilities (Green 1995; Pagel and Meade 2006) as opposed to only the rate parameters being sampled in this way, as in conventional MCMC (Pagel et al. 2004). We used an exponentially distributed hyperprior (see Pagel et al. 2004) with its mean value seeded from a uniform distribution with an interval that contained, but did not determine, the posterior distribution. To avoid autocorrelation and allow exploration of ample parameter space, we varied the amount by which the rate parameters are allowed to change between iterations of the Markov chain ('ratedev') until acceptance rates averaged 20-40%. Due to initially low acceptance rates we used a modified version of the code that accepts either a move to a new model or a move to a different tree in each iteration, rather than both simultaneously (courtesy of A. Meade). We ran 50×10^6 generations, sampling every 1,000 generations, yielding a sample of 49,000 iterations after 1×10^6 iterations were removed as burnin.

Awn loss and clade size

Sister clade comparisons were carried out to estimate differences in clade size between awned and awnless clades. Based on the ancestral state reconstructions under parsimony and mcmc 12 sister clade comparisons were made; based on the ML reconstructions 13 comparisons were made. Differences in diversity were assessed with Wilcoxon's signed rank test and a sign test, with average clade sizes across the same sample of 1,000 trees as input. To incorporate a test with an evolutionary null model, we tested for imbalances in clade size beyond those expected from stochastic

differences resulting from random speciation/extinction processes, using equation 14 of Slowinski and Guyer (1989b). We did not include unsampled species in this test because although we are confident about their placement at the genus level we do not wish to guess their placement among the tips of the phylogeny.

Timing of awn loss events

Node ages of the 93 nodes defined in the ancestral state reconstruction (above), plus of 12 nodes leading to awn loss along a tip branch, were extracted from results of a recent dating analysis (A. Antonelli, unpublished results). Each node age (95% confidence interval (CI) of variation) was associated with a '0' or '1' based on the reconstructed ancestral state for that node. Equivocal nodes identified in the parsimony analyses were coded as (1) whereas equivocal nodes identified in the ML and Bayesian optimisations were coded as (0). This maximised overlap among the three sets of nodes coded as (1) that were used for the following analysis (27 nodes under parsimony, 25 under mcmc, 22 under ML).

To assess whether the sequence of awn loss events in time is more clustered than would be expected by chance the classical runs test, recently brought into a phylogenetics context by Ford et al. (2009), would seem appropriate. However, we note that this test does not take the length of the runs into account, meaning that in the present data set, the long run of '0's that separates the root at 26.1 Ma from the first awn loss event at 6.37—3.53 Ma is weighted no differently from a run constituting a single '0' occurring toward the more recent end of the sequence. Instead we generated a null distribution of nodes ages associated with awn loss events ('1's) by replicating the sequence of presence/absence data ('0's and '1's) 100 times and permuting each sequence. This generates a null distribution sampled from all observed node ages of the Danthonioideae. We tested whether the observed distribution of node ages associated with '1's differed significantly from the expected using the Wilcoxon rank sum test, separately for minimum and maximum 95% CI ages. This tests the probability that the two samples come from the same distribution and is appropriate in this case where sample sizes differ and where the data are not normally distributed.

Correlation analyses: awns and life history

Most species in Danthonioideae are awned and perennial but awnless species appear to constitute a high proportion of annual species (Table 1). To test whether evolution of awns is correlated with the evolution of life history we compared the fit of dependent and independent models of evolution to the data using the Discrete (ML) and BayesDiscrete commands (Pagel 1994; Pagel and Meade 2006) in BayesTraits. Eight rate parameters constitute the dependent model. These allow each character to evolve at different rates, both for forward and backward shifts, depending on the state of the second character. In the independent model, shifts in one character occur at the same rate regardless of the state of the second parameter (coefficients $q12=q34$, $q13=q24$, $q21=q43$ and $q31=q42$; see definitions in Table 2). Hence, a model of independent evolution has four parameters. We ran one analysis in which rate parameters were allowed to vary freely and one analysis in which sampling of models was restricted to sampling only independent models. Fit of dependent and independent models were compared with a LR test under ML (Edwards 1972) and with Bayes factors (BF) under rj-mcmc (Raftery 1996). The BF is calculated as twice the difference in log harmonic mean of the worst and best fitting models. To ensure that the harmonic mean remained stable within and among runs multiple, long analyses were performed (A. Meade, pers. comm.). Priors were selected and nodes were defined as described above. For the dependent analyses we ran 150×10^6 iterations, sampling every 1,000 iterations, yielding a sample of 110,000 iterations after

burnin was removed. For the independent analyses we ran 100 x 10^6 iterations, sampling every 1,000 iterations, yielding a sample of 90,000 iterations after burnin was discarded. For the ML analysis we carried out 1,000 ML iterations per tree.

Table 2. Definition of rate coefficients compared in rj-mcmc correlation analyses.

Coefficient	Evolutionary transition
Forward shifts (0→1):	
q_{12}	Shift into annual in an awned background
q_{13}	Loss of awn in a perennial background
q_{24}	Loss of awn in an annual background
q_{34}	Shift into annual in unawned background
Backward shifts (1→0):	
q_{21}	Shift back to perennial in awned background
q_{31}	Secondary gain of awn in perennial background
q_{42}	Secondary gain of awn in annual background
q_{43}	Shift back to perennial in unawned background

The influence of *Tribolium* and *Schismus*

Awnless, annual species are concentrated in *Tribolium* and *Schismus*. To test the influence of these two clades on the overall results we pruned both lineages from the set of 1,000 trees as before and repeated the analyses above. Ancestral state reconstruction was carried out with 1 x 10^6 iterations of ML analysis or 100 x 10^6 iterations of rj-mcmc analysis, sampling every 1,000 iterations, yielding a sample of 90,000 iterations after removal of burnin. Nodes were defined as for the entire data set, excluding the 14 nodes in *Tribolium* and *Schismus*. Sister clade comparisons of clade size (parsimony 11, ML: 12, rj-mcmc: 10) were repeated and differences were evaluated with Wilcoxon's signed rank test and a sign test. Analysis of the sequence in time of awn loss events was based on 90 nodes, of which 14, 15 or 17 were coded as '1' (parsimony, ML and rj-mcmc, respectively). Analyses of correlated evolution between the awn and life history characters was performed with 1,000 ML iterations per tree or 200 x 10^6 iterations of rj-mcmc, sampling every 1,000 iterations, yielding a sample of 140,000 iterations after burning was discarded.

Quantification of variation in associated diaspore traits

To quantify morphological attributes of the diaspores associated with the absence of an awn we separated awned and awnless species into two groups. Each of these groups was then subdivided again, separating species villous lemma backs and species with glabrous lemma backs. The number of species in each group was counted. The subdivision was repeated, instead separating species with villous calli and species with glabrous calli. The number of species in each group was recounted. Independence of the frequency of glabrous lemmas and calli in awned species compared to in unawned species was assessed with Pearson's chi-square test with one degree of freedom. The total number of cases in each test was 280.

We also quantified the difference in the distribution of callus length variation between awned and unawned species using the non-parametric Wilcoxon rank sum test and using minimum and maximum recorded callus lengths as input. Data on callus length are not available for 75 (27%) of all Danthonioideae species and filling this gap would be beyond the scope of the present study. However, because species for which data are available constitute 13% unawned species, which is an accurate representation of the 14% unawned species in the entire dataset, we do not expect this to bias the results.

Results

Taxon sampling and phylogeny

The standard deviation of split frequencies in the six independent MrBayes runs stabilised at 0.03 (for chain temperatures of 0.1 and 0.2) and 0.04 (temperature 0.3). The effective sample size of the combined post burn-in tree samples (11,406 trees) was 305, i.e. far above the recommended minimum 100 for a reliable analysis (Drummond and Rambaut 2007). All six runs reached a plateau at the same log likelihood value (Fig. S1A-C, online appendix). The topology expected from previous analyses (Pirie et al. 2008), with improved resolution in the Rytidosperma clade (Humphreys et al. 2010) was successfully recovered (Fig. S2, online appendix). This means the phylogenetic hypothesis remains robust under addition of both taxa and data and lends confidence to its predictiveness. Therefore, it seems unlikely that addition of missing species will have a large impact on overall patterns inferred below.

Number of inferred awn loss events and rate parameters

All three methods of character optimisation found support for an asymmetrical model of evolution (Table 3A). Under parsimony awns are lost on average eight times more than they are regained, but this imbalance is less severe than the one expected from the permuted data where awn loss occurs on average 18 times more than secondary gain occurs. These results suggest that awn loss is phylogenetically constrained. Under ML (support for asymmetrical model $P<0.001$, under a chi-square distributed null and 1 d.f.) forward rates were in the same range as the number of shifts inferred using parsimony, but backward rates were much higher. In a Bayesian framework only asymmetrical models were sampled and forward rates were more variable, while backward rates were intermediate compared to those inferred with parsimony and ML (Table 3A).

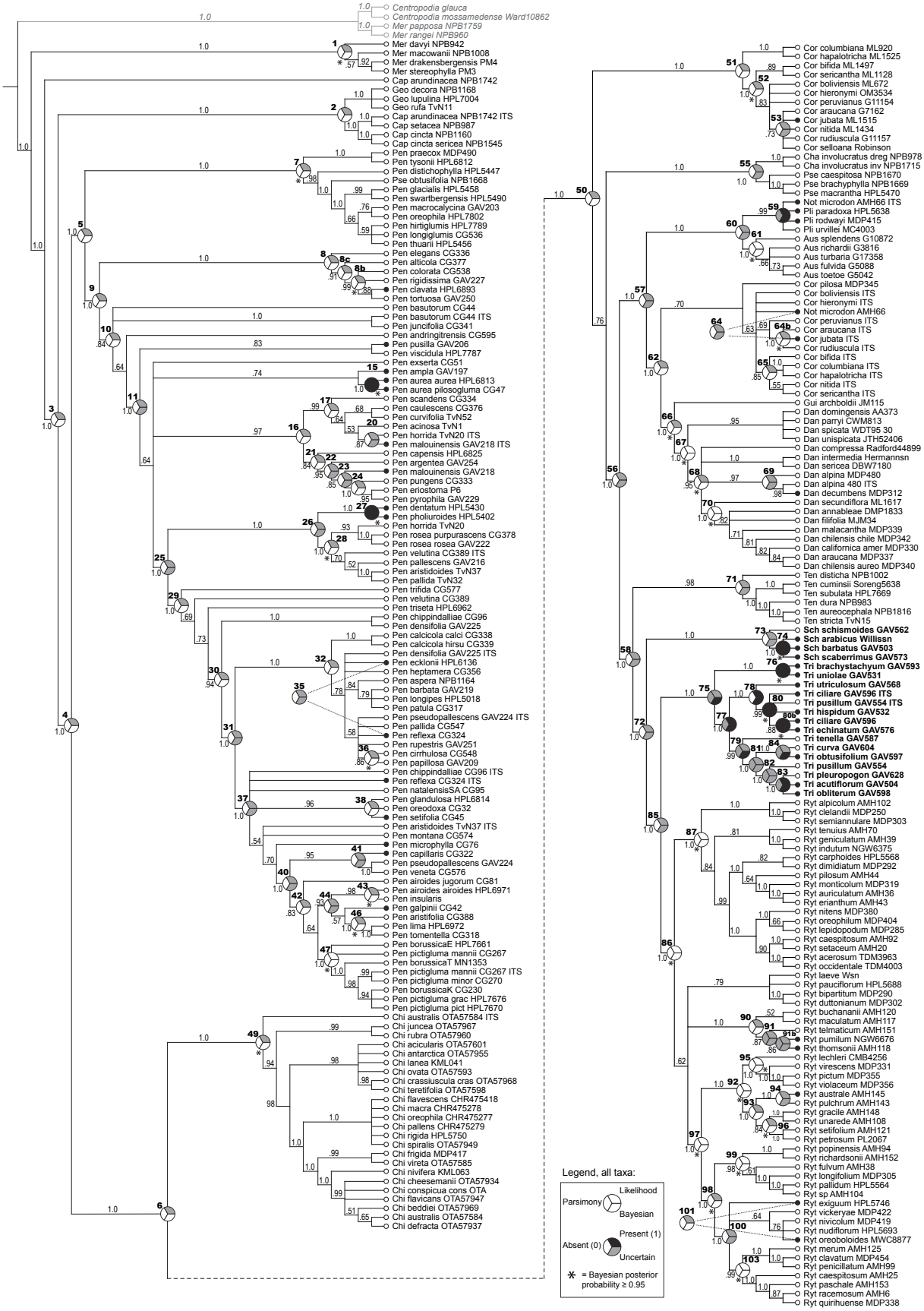
Table 3. Forward and backward shifts in the evolution of awns inferred under parsimony, ML and rj-mcmc. Observed numbers of awn loss events ([0→1]) and secondary gains ([1→0]) and rate parameters ($q01$, $q10$) estimated under different models of evolution. Permuted data were analysed only under parsimony. **A.** All taxa. **B.** Excluding *Tribolium* and *Schismus*.

A. Entire data set.

Parameter	**parsimony:** 95% confidence interval (mean)	**ML:** 95% confidence interval (mean)	**rj-mcmc:** 95% confidence interval (mean)
Observed [0→1]; $q01$	24-30 (27.2)	25.00-32.88 (28.56)	14.45-39.20 (25.64)
Permuted [0→1]	32-41 (37.0)	-	-
Observed [1→0]; $q10$	1-7 (3.37)	89.80-145.0 (119.1)	13.46-158.20 (68.00)
Permuted [1→0]	0-6 (2.11)	-	-

B. *Tribolium* and *Schismus* removed.

Parameter	**parsimony:** 95% confidence interval (mean)	**ML:** 95% confidence interval (mean)	**rj-mcmc:** 95% confidence interval (mean)
Observed [0→1]; $q01$	21-24 (22.7)	31.08-127.7 (63.73)	15.28-121.1 (59.73)
Permuted [0→1]	23-28 (26.2)	-	-
Observed [1→0]; $q10$	0-3 (1.23)	204.4-1000 (475.9)	112.0-915.9 (423.1)
Permuted [1→0]	0-3 (0.741)	-	-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Mer stereophylla PM3
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Pen juncifolia CG341
Pen andringitrensis CG595
Pen pusilla GAV206
Pen viscidula HPL7787
Pen exserta CG51
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Pen scandens CG334
Pen caulescens CG376
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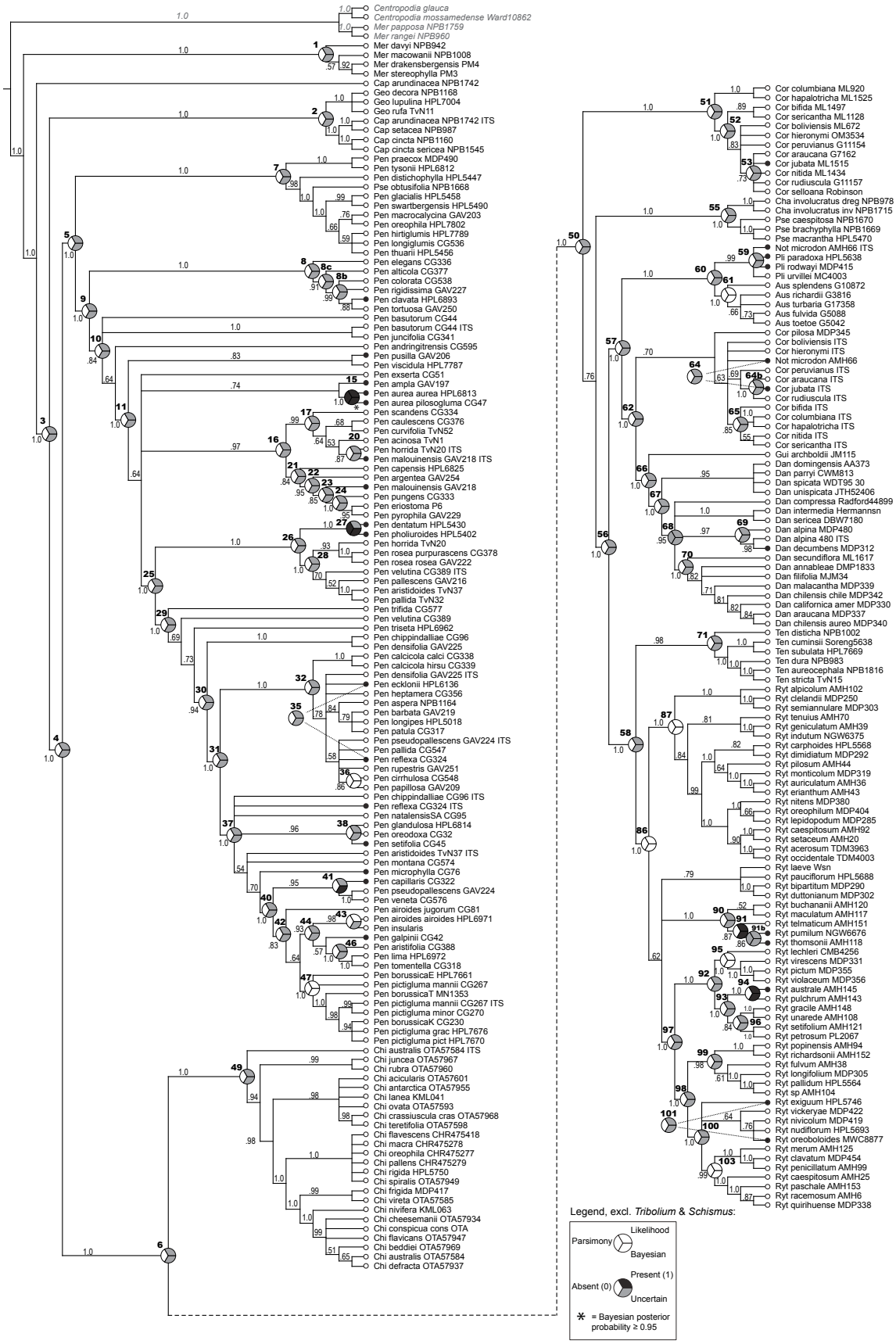
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Pen caulescens CG376
Pen curvifolia TvN52
Pen acinosa TvN1
Pen horrida TvN20 ITS
Pen malouinensis GAV218 ITS
Pen capensis HPL6825
Pen argentea GAV254
Pen malouinensis GAV218
Pen pungens CG333
Pen eriostoma P6
Pen pyrophila GAV229
Pen dentatum HPL5430
Pen pholiuroides HPL5402
Pen horrida TvN20
Pen rosea purpurascens CG378
Pen rosea rosea GAV222
Pen velutina CG389 ITS
Pen pallescens GAV216
Pen aristidoides TvN37
Pen pallida TvN32
Pen trifida CG577
Pen velutina CG389
Pen triseta HPL6962
Pen chippindalliae CG96
Pen densifolia GAV225
Pen calcicola calci CG338
Pen calcicola hirsu CG339
Pen densifolia GAV225 ITS
Pen ecklonii HPL6136
Pen heptamera CG356
Pen aspera NPB1164
Pen barbata GAV219
Pen longipes HPL5018
Pen patula CG317
Pen pseudopallescens GAV224 ITS
Pen pallida CG547
Pen reflexa CG324
Pen rupestris GAV251
Pen cirrhulosa CG548
Pen papillosa GAV209
Pen chippindalliae CG96 ITS
Pen reflexa CG324 ITS
Pen natalensisSA CG95
Pen glandulosa HPL6814
Pen oreodoxa CG32
Pen setifolia CG45
Pen aristidoides TvN37 ITS
Pen montana CG574
Pen microphylla CG76
Pen capillaris CG322
Pen pseudopallescens GAV224
Pen veneta CG576
Pen airoides jugorum CG81
Pen airoides airoides HPL6971
Pen insularis
Pen galpinii CG42
Pen aristifolia CG388
Pen lima HPL6972
Pen tomentella CG318
Pen borussicaE HPL7661
Pen pictigluma mannii CG267
Pen borussicaT MN1353
Pen pictigluma mannii CG267 ITS
Pen pictigluma minor CG270
Pen borussicaK CG230
Pen pictigluma grac HPL7676
Pen pictigluma pict HPL7670
Chi australis OTA57584 ITS
Chi juncea OTA57967
Chi rubra OTA57960
Chi acicularis OTA57601
Chi antarctica OTA57955
Chi lanea KML041
Chi ovata OTA57593
Chi crassiuscula cras OTA57968
Chi teretifolia OTA57598
Chi flavescens CHR475418
Chi macra CHR475278
Chi oreophila CHR475277
Chi pallens CHR475279
Chi rigida HPL5750
Chi spiralis OTA57949
Chi frigida MDP417
Chi vireta OTA57585
Chi nivifera KML063
Chi cheesemanii OTA57934
Chi conspicua cons OTA
Chi flavicans OTA57947
Chi beddiei OTA57969
Chi australis OTA57584
Chi defracta OTA57937
Cor columbiana ML920
Cor hapalotricha ML1525
Cor bifida ML1497
Cor sericantha ML1128
Cor boliviensis ML672
Cor hieronymi OM3534
Cor peruvianus G11154
Cor araucana G7162
Cor jubata ML1515
Cor nitida ML1434
Cor rudiuscula G11157
Cor selloana Robinson
Cha involucratus dreg NPB978
Cha involucratus inv NPB1715
Pse caespitosa NPB1670
Pse brachyphylla NPB1669
Pse macrantha HPL5470
Not microdon AMH66 ITS
Pli paradoxa HPL5638
Pli rodwayi MDP415
Pli urvillei MC4003
Aus splendens G10872
Aus richardii G3816
Aus turbaria G17358
Aus fulvida G5088
Aus toetoe G5042
Cor pilosa MDP345
Cor boliviensis ITS
Cor hieronymi ITS
Not microdon AMH66
Cor peruvianus ITS
Cor araucana ITS
Cor jubata ITS
Cor rudiuscula ITS
Cor bifida ITS
Cor columbiana ITS
Cor hapalotricha ITS
Cor nitida ITS
Cor sericantha ITS
Gui archboldii JM115
Dan domingensis AA373
Dan parryi CWM813
Dan spicata WDT95 30
Dan unispicata JTH52406
Dan compressa Radford44899
Dan intermedia Hermannsn
Dan sericea DBW7180
Dan alpina MDP480
Dan alpina 480 ITS
Dan decumbens MDP312
Dan secundiflora ML1617
Dan annableae DMP1833
Dan filifolia MJM34
Dan malacantha MDP339
Dan chilensis chile MDP342
Dan californica amer MDP330
Dan araucana MDP337
Dan chilensis aureo MDP340
Ten disticha NPB1002
Ten cuminsii Soreng5638
Ten subulata HPL7669
Ten dura NPB983
Ten aureocephala NPB1816
Ten stricta TvN15
Ryt alpicolum AMH102
Ryt clelandii MDP250
Ryt semiannulare MDP303
Ryt tenuius AMH70
Ryt geniculatum AMH39
Ryt indutum NGW6375
Ryt carphoides HPL5568
Ryt dimidiatum MDP292
Ryt pilosum AMH44
Ryt monticolum MDP319
Ryt auriculatum AMH36
Ryt erianthum AMH43
Ryt nitens MDP380
Ryt oreophilum MDP404
Ryt lepidopodum MDP285
Ryt caespitosum AMH92
Ryt setaceum AMH20
Ryt acerosum TDM3963
Ryt occidentale TDM4003
Ryt laeve Wsn
Ryt pauciflorum HPL5688
Ryt bipartitum MDP290
Ryt duttonianum MDP302
Ryt buchananii AMH120
Ryt maculatum AMH117
Ryt telmaticum AMH151
Ryt pumilum NGW6676
Ryt thomsonii AMH118
Ryt lechleri CMB4256
Ryt virescens MDP331
Ryt pictum MDP355
Ryt violaceum MDP356
Ryt australe AMH145
Ryt pulchrum AMH143
Ryt gracile AMH148
Ryt unarede AMH108
Ryt setifolium AMH121
Ryt petrosum PL2067
Ryt popinensis AMH94
Ryt richardsonii AMH152
Ryt fulvum AMH38
Ryt longifolium MDP305
Ryt pallidum HPL5564
Ryt sp AMH104
Ryt exiguum HPL5746
Ryt vickeryae MDP422
Ryt nivicolum MDP419
Ryt nudiflorum HPL5693
Ryt oreoboloides MWC8877
Ryt merum AMH125
Ryt clavatum MDP454
Ryt penicillatum AMH99
Ryt caespitosum AMH25
Ryt paschale AMH153
Ryt racemosum AMH6
Ryt quirihuense MDP338
Legend, excl. Tribolium & Schismus:
Likelihood
Parsimony
Bayesian
Present (1)
Absent (0)
Uncertain
* = Bayesian posterior probability ≥ 0.95

Figure 2. Ancestral state reconstructions shown on the Bayesian majority rule consensus tree. Ancestral node reconstructions at each node are shown as a pie chart split into three, each slice representing the results of the three different methods employed: parsimony, ML and rj-mcmc. For details of the support for the results presented, refer to the text and Appendix II. **A.** All taxa. **B.** Excluding *Tribolium* and *Schismus*.

Ancestral state reconstruction of awns

Ancestral states reconstructed for each node using parsimony, ML and rj-mcmc are presented in detail in Appendix II and summarised in Fig. 2A. For 83 out of 93 nodes, parsimony analysis provided unambiguous assignment of one or the other state across all trees. Relative likelihoods of a node adopting a particular state are summarised as mean values for each node. A plot of the mean likelihood values for each node adopting state (1) against node number reveals two gaps in the distribution of likelihood values, corresponding to the ten highest and ten lowest values, respectively. The ten highest likelihood values (0.93-1.0) were interpreted as signifying state (1) and the ten lowest values (0.0055-0.049) as signifying state (0). Ancestral state of the remaining 73 nodes was considered uncertain (Fig. 2). Under rj-mcmc ancestral states were considered unambiguous if the mean (± standard deviation) posterior probability for a node adopting a state was ≥ 0.95 (Appendix II). Accordingly, the presence of an awn was reconstructed with certainty at 24 nodes and the absence of an awn was reconstructed with certainty at seven nodes. Ancestral states of 62 nodes are ambiguous according to these measures. Nodes reconstructed with a p.p. ≤ 0.80 have been indicated in Fig. 2, to indicate further trends in the data.

Presence of an awn was inferred at the root node under parsimony and there was weak support for the presence of an awn under rj-mcmc (p.p.=0.71) but not under ML (proportional likelihood [0]=0.54). Restricting the likelihood model to a single rate parameter increased the likelihood of the presence of an awn at the root to 0.86, but such a model was not supported by the data (LR test, $P>0.05$). Restricting the root node to (0) did not change the overall likelihood of the model but then neither did restricting the root node to (1) (LR test, $P>0.05$).

Diversity of unawned clades compared to their sisters

Species diversity in awnless clades was lower than the diversity of their awned sister clades, regardless of ancestral state reconstruction method (Fig. 3A). However, these differences are not statistically significant ($P>0.05$ for all three tests). Awnless clades contained fewer species than their sisters in five of the cases compared, six cases revealed no difference in size (tip events occurring within one of the members of a single species pair) and in one (node 74 [Fig. 2A], parsimony, mcmc) or two (nodes 74 and 83 [Fig. 2A], ML) comparisons awnless clades contained more species than their awnless sisters. Low phylogenetic support in some clades limited the number of sister clade comparisons that could be made.

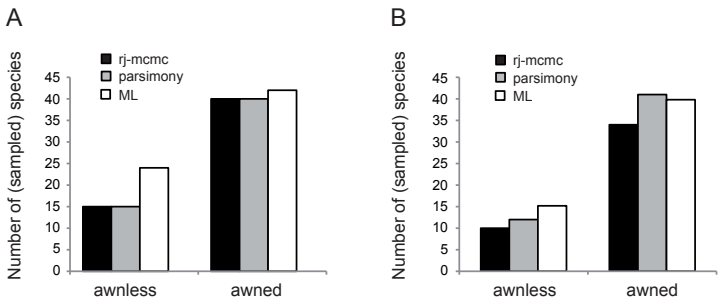

Figure 3. Total diversity of awnless clades compared to the total diversity of their awned sister clades, displayed separately for each ancestral state reconstruction method. The differences are not statistically significant. **A.** All taxa. **B.** Excluding *Tribolium* and *Schismus*.

Timing of awn loss events

Age of each of the defined nodes is shown in Appendix II. The distribution of ages associated with the absence of an awn is significantly younger than expected by chance (Wilcoxon rank sum test, n_1=27, n_2=2700, W=25183, *P*=0.006 [min. ages], W=24489, *P*=0.003 [max. ages]) (Fig. 4A). We only carried out this test based on ages of awnless nodes inferred under parsimony because the distribution of ages did not differ compared to those inferred with the other two methods (Wilcoxon rank sum test, ML: n_1=18, n_2=22, W=226, *P*=0.45 [min. ages], W=221, *P*=0.54 [max. ages], rj-mcmc: n_1=18, n_2=25, W=181.5, *P*=0.29 [min. ages], W=186, *P*=0.34 [max. ages]).

Correlation analyses: awns and life history

Both ML and rj-mcmc analyses found a better fit of a dependent model of evolution over a model of independent evolution (ML: $P < 0.01$ LR test statistic compared to a X^2 distribution, with four degrees of freedom, considering the 95% CI of the likelihood values across trees; rj-mcmc: logBF = 16.2) (Table 4). Comparison of rate parameters of the dependent model reveals that shifts from perennial to annual do not occur in an awned background ($q12=0$) but occur frequently in an awnless background ($q34>0$). Consistently with this, awn loss is inferred to occur before a shift into an annual life history ($q13 > q12$). None of the backward rate parameters ($q21$, $q31$, $q42$ and $q43$) can be distinguished from each other. These differences are illustrated in Table 5A.

Individual node reconstructions under a dependent model of evolution are shown in Fig. S3 (online appendix). The prevalent character combination (awn present; perennial) is reconstructed for one node each in *Pentameris* and *Danthonia*, three nodes in *Rytidosperma* and ancestrally in *Austroderia* and *Rytidosperma* ($p.p \geq 0.95$, nodes 47, 67, 87, 95, 103, 61 and 86 in Fig. S3). In addition absence of an awn and a perennial life history is reconstructed at node 15 ($p.p \geq 0.95$). Considering also nodes reconstructed with $p.p \geq 0.80$, reveals that awn loss probably also occurred in perennial lineages (*Notochloe/Plinthanthesis* and in *Tribolium*), consistent with the findings above. However, annuals have also evolved in awned lineages (in *Pentameris*).

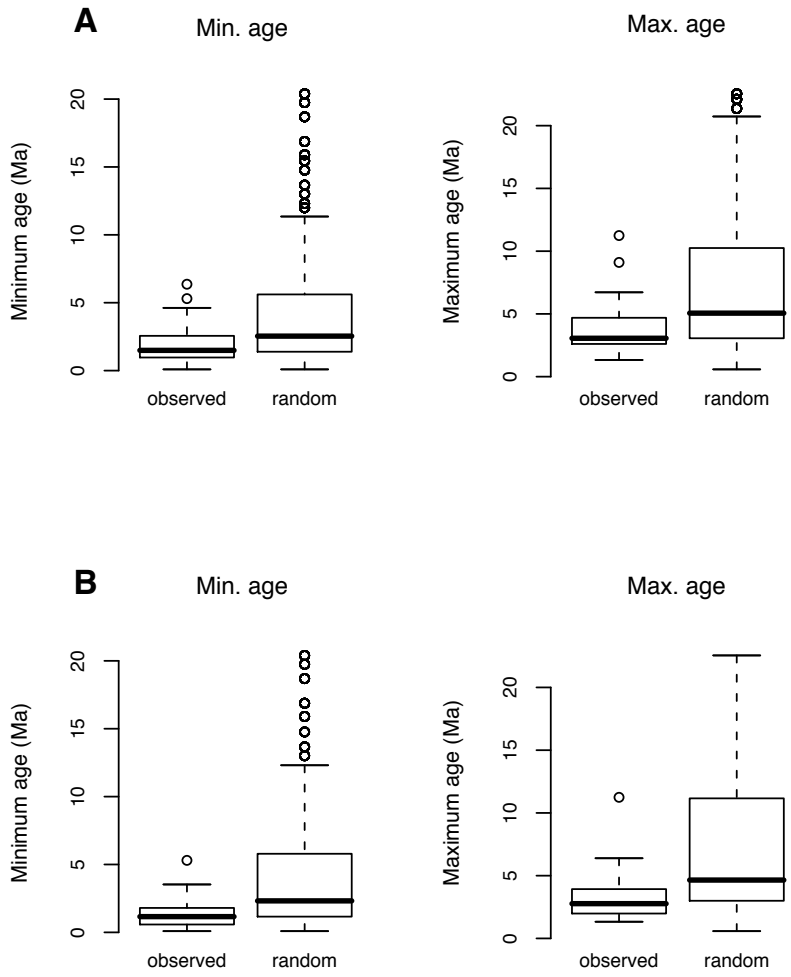

Figure 4. Distribution of observed minimum (left) and maximum (right) ages of awn loss events for the entire data set (A) and excluding *Tribolium* and *Schismus* (B). Differences between observed and randomised ages (see text for explanation) are significant at $P < 0.0.1$ using Wilcoxon's rank sum test. These differences suggest that awn loss events have occurred more recently than expected by chance.

Table 4. Statistics of dependent (D) and independent (I) models of evolution between awn and life history. A. All taxa. Dependent models were sampled 48,999 times and independent models were sampled only twice. B. Excluding *Schismus* and *Tribolium*. Dependent models were sampled in all of the rj-mcmc iterations.

Data	Mean log L(I)	Mean log L(D)	LR significance level X^2 with 4 d.f.	Log harmonic mean (I)	Log harmonic mean (D)	*n* models [D/I]	Log-BF[1]
A	-166.67	-159.09	0.01	-164.18	-156.08	48,999/2	16.2
B	-125.95	-121.99	*n.s.*	-128.47	-119.89	49,001/0	17.2

[1]On a logarithmic scale values of 2-5 are considered 'positive' evidence that the models are different, values greater than 5 are 'strong evidence' and values greater than 10 are 'very strong evidence' (Raftery, 1996; Pagel & Meade, 2006).

Table 5. Top five models in the posterior sample of dependent models, along with their posterior density frequencies (PDF), cumulative density frequencies (CDF) and the rate classes of the constituent rate coefficients. Z=rate category zero; 0=first positive rate class; 1=second positive rate class. Forward rate parameters are marked in bold. **A.** All taxa. In total, 985 models were sampled and the five most frequently sampled models account for 51% of the iterations. The 95% percentile of the model space contains models with the rate coefficients in two or three rate categories (average 2.01). The $q12$ parameter is in the zero bin in almost all models, $q13$ is mostly found in the first rate category and $q34$ is in either the first or second rate category. None of the reversal rates can be distinguished. **B.** Excluding *Tribolium* and *Schismus*. In total, 956 models were sampled and the five most frequently sampled models account for 53% of the iterations. The 95% percentile of the model space contains models with the rate coefficients in two or three rate categories (average 2.05). As in the analysis of the entire data set the $q12$ rate coefficient is almost always in the zero bin and thus distinguishable from coefficients $q13$ and $q34$. Rate parameters are overall variable and no further inferences can be made based on the rate parameters.

A. All taxa

Model	$\boldsymbol{q_{12}}$	$\boldsymbol{q_{13}}$	q_{21}	$\boldsymbol{q_{24}}$	q_{31}	$\boldsymbol{q_{34}}$	q_{42}	q_{43}	PDF	CDF
1	Z	0	1	1	1	1	1	1	0.18	0.18
2	Z	0	1	0	1	1	1	1	0.15	0.32
3	Z	0	1	0	0	1	1	1	0.07	0.40
4	Z	0	1	1	1	0	1	0	0.06	0.46
5	Z	0	1	0	1	0	1	0	0.05	0.51
q occurrence in rate class	99.5%	84%	77%	0: 45% 1: 45%	0: 27% 1: 63%	0: 31% 1: 67%	80%	0: 28% 1: 69%		

B. Excluding *Tribolium* and *Schismus*

Model	$\boldsymbol{q_{12}}$	$\boldsymbol{q_{13}}$	q_{21}	$\boldsymbol{q_{24}}$	q_{31}	$\boldsymbol{q_{34}}$	q_{42}	q_{43}	PDF	CDF
1	Z	0	1	1	1	0	1	0	0.15	0.15
2	Z	0	1	0	1	0	1	0	0.12	0.27
3	Z	0	1	0	1	0	1	Z	0.11	0.39
4	Z	0	1	1	1	0	1	Z	0.08	0.47
5	Z	1	0	1	0	1	0	1	0.06	0.53
q occurrence in rate class	99.6%	0: 75% 1: 25%	0: 30% 1: 62%	0: 38% 1: 55%	0: 25% 1: 72%	0: 72% 1: 27%	0: 25% 1: 73%	0: 38% 1: 31% Z: 29%		

Removal of *Tribolium* and *Schismus*

Ancestral states found when *Tribolium* and *Schismus* were excluded from the analysis are shown in Fig. 2B and in detail in Appendix II. Overall the patterns match those found in the entire data set but ancestral states of fewer nodes are reconstructed unambiguously. Neither forward nor backward shifts inferred under parsimony could be distinguished from those expected from the permuted data (Table 3B). Rate parameters estimated under ML and rj-mcmc were highly variable and suggest very high forward rates and extremely high backward rates compared to parsimony (Table 3B). The root was reconstructed as being awned under parsimony but it was ambiguous under ML and rj-mcmc (ML(0) = 0.50; p.p. (0) = 0.51). Restricting the ML model to a single rate parameter increased the certainty of the state at the root (ML(0) = 0.94), but that model was not supported by the data (LR test, $P < 0.001$, 1 d.f.).

Awnless clades were smaller than their awned sisters under all three methods of ancestral state reconstruction (Fig. 3B), but these differences were not significant (Wilcoxon's signed rank test and sign test, P=0.06-0.13, with 9-11 d.f.). Awnless clades

contained fewer species than their sisters in five (parsimony, ML) or four (mcmc) of the cases compared and six cases revealed no difference in size (tip events occurring within one of the members of a single species pair). Only at one node did awnless clades contained more species than their awnless sisters and this was reconstruction was only recovered under ML analyses (node 91 [Fig. 2B], ML).

Awn loss occurred significantly more toward the present than expected by chance (Wilcoxon rank sum test, n_1=15, n_2=1500, W=6326, *P*=0.003 (min. ages), W=6611, *P*=0.006 (max. ages)) (Fig. 4B). Ages inferred based on the different ancestral state reconstructions were not significantly different (Wilcoxon rank sum test, ML: n_1=14, n_2=15, W=94, *P*=0.89 (min. and max. ages), rj-mcmc: n_1=14, n_2=17, W=114.5, *P*=0.88 (min. ages), W=118.5, *P*=0.75 (max. ages)).

Correlation analyses based on ML revealed no difference in fit between a dependent and independent model of evolution (P > 0.05, LR test statistic compared to a X^2 distribution with 4 d.f.) whereas under rj-mcmc a dependent model fits the data much better (logBF = 17.2) (Table 4B). Comparison of rate parameters again reveals that q12 = 0 and q13 > 0, suggesting that awn loss occurs before evolution of an annual life history and that q34 > 0 indicating that shifts to being annual occur in an awnless background but not an awned background (Table 5B).

Variation in associated diaspore traits

The frequency of glabrous lemmas or calli differs significantly between awned and awnless species. A higher proportion of awnless species have glabrous lemma backs (Table 6A: 11% of awnless versus 2.9% of awned species; Pearson's chi-square test with 1 d.f., *P* = 0.024) and glabrous calli (Table 6B: 42% of awnless versus 0.39% of awned species; Pearson's chi-square test with 1 d.f., *P* < 0.0001). Only two species have both a glabrous lemma and a glabrous callus and the data show no significant skew when awn presence or absence is not taken into account (Table 6C).

Overall callus length ranges from 0.01 mm (*Rytidosperma australe*) to 4 mm (*Pseudopentameris macrantha, P. caespitosa*). Separated into pools of awn presence or absence, callus length ranges 0.1–4 mm in awned species and 0.01–0.75 mm in awnless species (Fig. 5). Thus, short calli occur among both awned and awnless species but awnless species never have long calli. This difference is highly significant (Wilcoxon rank sum test, n_1=26, n_2=179, W=536 (min lengths; 518 for max lengths), *P* < 0.0001) and is independent of whether minimum or maximum callus lengths are analysed.

Table 6. Quantification of the awn-callus-lemma 'burial syndrome'. Frequency of occurrence of lemma (A) and callus (B) indumentum tested against the present or absence of an awn and tested against each other (C). Significance levels of Pearson's chi-square test: * = significant at P = 0.05; *** = significant below P = 0.0001; *n.s.* = not significant.

A	Lemma villous	Lemma glabrous *
Awn present	235	7
Awn absent	34	4

B	Callus villous	Callus glabrous ***
Awn present	241	1
Awn absent	22	16

C	Lemma villous	Lemma glabrous *n.s*
Callus villous	254	9
Callus glabrous	15	2

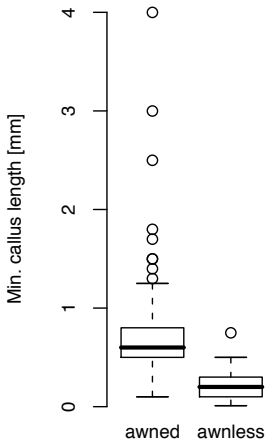

Figure 5. Distribution of minimum callus length compared between awned and awnless species. Differences are significant at $P < 0.0001$ using Wilcoxon's rank sum test and indicate that the length of the callus is one of the traits involved in the 'burial syndrome'.

Discussion

Ancestral state reconstruction and the evolution of awns in Danthonioideae

Contrary to other recent studies (e.g. Ekman et al. 2008) we found a surprising amount of agreement among methods of ancestral state reconstruction. All three methods resulted in the inference of the absence of an awn at two nodes within *Pentameris* (nodes 15 and 27) and several nodes within *Tribolium* and *Schismus* (Fig. 2). None of the models found support for ancestral absence of an awn in any of the other genera and all three methods support the presence of an awn ancestrally in all (parsimony, mcmc) or most (ML) of the genera or their major constituent clades. All three methods found similar rates of forward change (Table 3), with the increased variability around the mean for the ML and mcmc analyses representing the greater degree to which these methods account for uncertainty in the process of character change (Pagel 1994; Nielsen 2002; Huelsenbeck et al. 2003). Backward shifts (secondary gains) however, differed tremendously among methods (Table 3). Under parsimony one to seven reversals are inferred, depending on phylogenetic resolution, while ML and mcmc reconstructions require highly variable and on average very high reversal rates to explain the data.

Parsimony is known to provide a reasonable reconstruction of evolutionary patterns when rates of evolution are low (Harvey and Pagel 1991; Pagel 1999; Huelsenbeck et al. 2003). Our phylogenetic reconstruction of the Danthonioideae reveals that one reversal may have taken place in the clade arising from node 59 (leading to *Plinthanthesis urvillei*), two or three reversals could have occurred in *Pentameris*, one to three in *Tribolium* and one or two in *Rytidosperma* (Fig. 2). Clearly, parsimony inferred reversals account for these patterns very well. However, rate parameters inferred under Markov-based models are not unexpected given the distance from the root node to the nodes where the first forward shifts (0 → 1) occur. To counter any stray 0 → 1 shifts at deeper nodes in the trees, reverse rates ($q10$) must be high (Pagel 1994, 1999). The reversal rates found in the present study are therefore probably an artefact of the Markov model, in which both rate parameters are assumed to take positive values ($q01$, $q10 > 0$) along all branches. In addition, short branches along which change is inferred to occur are likely to inflate rates further in the form of multiple 'unseen' changes along these branches (Pagel 1994).

Awns are absent in 38 species of Danthonioideae and are inferred to have been lost repeatedly, on average 25.6 (rj-mcmc), 27.2 (parsimony) or 28.6 (ML) times. This rate of awn loss is significantly lower than expected by chance (Table 3). A tempting interpretation of this is that there has been selection against awn loss such that most lineages in which awn loss occurs do not persist and leave detectable traces of these events. In support of this we found that multiple awnless species are scattered in *Cortaderia*, *Danthonia, Notochloe*, *Pentameris*, *Plinthanthesis* and *Rytidosperma* and are phylogenetically clustered only in *Tribolium* and *Schismus*. Garnier and Dajoz (2001) demonstrated that different awn lengths are inherited intraspecifically in *Hyparrhenia diplandra*, suggesting that awn characteristics have a genetic, heritable basis. In the Danthonioideae, by contrast, much of the pattern surrounding the absence of an awn on a macroevolutionary scale appears stochastic, the awnless state perhaps only being inherited in *Tribolium* and *Schismus*.

The ecological disadvantage of not having an awn applies also in an evolutionary context

Awnless clades in the Danthonioideae contain fewer species than their awned sisters (Fig. 3). Because sister clades are by default the same age and share most of their characteristics, size differences may reflect intrinsic differences, related to a character in which they differ, affecting their ability to diversify or propensity to go extinct (Barraclough et al. 1998). Galley and Linder (2007) also reported that loss of multicellular glands in orthophyllous lineages of *Pentameris*, but not in sclerophyllous lineages, led to fewer diversification events in these lineages. It is well known, however, that even seemingly dramatic imbalances between sister clades may have been generated by random speciation and extinction events alone (Raup et al. 1973; Slowinski and Guyer 1989b, a, 1993). Indeed, the differences in size of sister clades uncovered here are not statistically significant. The number of comparisons made in the present study was limited by lower phylogenetic resolution in some areas of the tree and a lack of statistical significance may also be the result of small sample sizes (Ree 2005). Repeatability may also constitute a measure of support for studies of this nature (de Queiroz 2002; Ree 2005) and we found that awnless clades contained fewer species than their sisters in five of the cases compared and only in one (parsimony, mcmc) or two (ML) comparisons did awnless clades contain more species than their awnless sisters. Importantly, both these nodes are within *Tribolium* (node 83, Fig. 2A) and *Schismus* (node 74, Fig. 2A) confirming that only in these genera does the awnless state persist and do awnless lineages diversify. Beyond these clades, the trend is that awnless clades contain fewer species than their awned sisters and if this pattern correlation is not due to stochasticity and indeed has an evolutionary, causal underpinning, then one of two evolutionary processes must explain it. Either awnless species speciate at a lower rate (low speciation rates) or they become extinct before speciating (ie. high extinction rates). Had we found that awnless clades were older than expected by chance, this would suggest persistence over evolutionary time with low turnover rates, allowing them to remain species-poor for long periods of time (Ricklefs 2003, 2005; Rabosky 2009a; Ricklefs 2009). Because we found that awn loss events have been more recent than expected by chance (Fig. 4), the lower diversity of awnless clades more likely reflects their recent occurrence (i.e. a condition often arising in a tip branch only) and by extrapolation, if any awn loss events occurred deeper in the tree any traces of these events will have been masked by high extinction rates, leading to a rapid turnover of lineages (Rabosky 2009a; Rabosky 2009b; Ricklefs 2009). Of course, reversals may also have masked traces of awn loss events deeper in the phylogeny. Both possibilities indicate that the ecological disadvantage of not having an awn also applies in an evolutionary context. To our knowledge our study provides the first documentation of the possible consequences of losing awns in an evolutionary context.

The 'burial syndrome'

A higher proportion of awnless danthonioid species have glabrous lemma backs or glabrous calli, with hardly any of the awned species being glabrous on these two parts of the diaspore (2.9% and 0.41%, respectively; Table 6). No association was found between lemma and callus indumentum if awn presence was not taken into consideration (Table 6) and only two species, both awnless, have both a glabrous callus and a glabrous lemma back. Further, awnless species on the whole have significantly shorter calli than awned species (Fig. 5). Consistently with this, Peart (1981) demonstrated that several characters act together with the awn to increase efficiency of burial, but importantly, these are only beneficial in the presence of an awn. In contrast, awnless "seeds" (here, diaspores) tend to lack most of these associated traits (Peart 1984). Together, these findings suggest that awns are the visible constituent of a compound morphological syndrome, the burial syndrome, involving a suite of diaspore traits. Under this interpretation, several morphological changes appear to act together over evolutionary time in the establishment of an ecological shift (Miller 1949), from active burial to reliance upon stochastic burial, enforced by the awnless state (Peart 1984).

Two extremes of the 'burial syndrome' occur in the Danthonioideae. In the first, caryopses are optimised toward active burial (Fig. 1B). Driven by the presence of a hygroscopically active awn, active burial is aided by a long, pointed callus that firmly anchors the caryopsis in the ground. Unidirectional movement into the soil is promoted by the presence of hairs on the lemma and callus that prevent upward movement (out of the soil) (Peart 1981). The other extreme is displayed by the awnless lemma that has a short callus and a glabrous lemma or callus, or both, culminating in a structure that is overall smaller, rounder and smoother (Fig. 1A). Such a structure is suited to reliance on stochastic burial (Peart 1984) that, in order to be successful, requires reduction or complete loss of features that would render landing or burial in any particular orientation 'wrong'. Because the association among these traits acts via the awn, we suggest that awn loss is the 'exaptation', i.e., the pre-requisite for evolution of the burial syndrome in the Gouldian sense (Gould and Vrba 1982). Further adaptations to the awnless state have occurred via subsequent changes in associated traits to increase efficiency of stochastic burial (Miller 1949; Gould and Vrba 1982; Baum and Larson 1991).

A well documented example of the evolution of a compound morphological 'syndrome' associated with an ecological shift is the evolution of wind pollination in plants. Wind pollinated plants are characterised by changes in a range of floral traits, which most prominently include condensation of the inflorescence, absence of nectar, reduced and colourless perianth parts, protruding stamens, dry pollen and solitary ovules (Faegri and Van der Pijl 1979; Linder and Rudall 2005). While several of these characters are significantly correlated with the evolution of wind pollination, dry pollen and perianth reduction seem to be necessary for the wind pollination syndrome to evolve – they constitute the exaptations (Linder 1998). Evolution of these key morphological changes probably allowed the ecological shift to wind pollination, the efficiency of which has been fine tuned following emergence of the syndrome, established through further adaptations to the newly opened niche. Other famous examples include the extreme fidelity with which the flowers of many orchid genera force visiting animals to behave in the exact way demanded for successful pollination (Van der Pijl and Dodson 1966) and the sequence of skeletal, feathering and body size modifications that led to powered flight in modern birds (Gould and Vrba 1982; Sereno 1999). In the same way, the interplay between the lemma awn, indumentum of the lemma and the callus and the length of the callus constitutes a burial syndrome, optimised toward efficient and reliable burial, enhancing successful germination and establishment.

How awnless species persist

Tribolium and *Schismus* both contain a high proportion of species without awns and a high proportion of annual species (Table 1), which are distributed in mostly semi-desert settings in Africa and the Mediterranean region (Linder and Davidse 1997; Linder et al. accepted manuscript). We uncovered an intriguing correlation between evolution of the awn character and life history such that a shift from perennial to annual is more likely in an awnless lineage than in an awned lineage. Annuals tend to increase in prevalence with increasing aridity (Charnov and Schaffer 1973; Axelrod 1979; Fiz et al. 2002; Verboom et al. 2003; Evans et al. 2005; Datson et al. 2008; Tank and Olmstead 2008) and are linked with climates with high seasonality (e.g. Verboom et al. 2004). The occurrence of annual species in the habitats of *Tribolium* and *Schismus* is therefore not surprising. Under these conditions adult survival is generally low and seedling survival high (Charnov and Schaffer 1973), meaning that annual species rely entirely on re-establishment from a viable seed bank after the passing of an unfavourably dry period, for their prolonged existence. How can it be, then, that the species that have lost the trait that is arguably the most important for ensuring renewed establishment in such habitats nevertheless persist?

In the absence of supporting experimental data, we speculate that the key to explaining this conundrum lies in the appreciation of the ecological shift bestowed by the two extremes of the burial syndrome: loss of the awn not only causes a shift from active to passive burial but also removes any preference for soil type (Peart 1981). Indeed, the species of *Tribolium* and *Schismus* occur on all sorts of soils (sandy soils, clay soils, well drained soils, seasonally flooded coastal sands) (Linder and Davidse 1997). Furthermore, numerous studies have shown that smaller and more spherical (compact) seeds tend to be more persistent (listed in Moles et al. 2000; Schwienbacher et al. 2010), probably because they are more easily buried and because burial confers persistence (Peart 1984; Thompson et al. 1993). A shift to a burial syndrome in which diaspores are smaller and therefore less costly to produce, while still allowing persistence of buried seeds, may therefore have allowed survival in habitats with temporarily unfavourable climates and on soils where hygroscopically active awns offer little benefit.

According to this explanation awnless lineages of *Tribolium* and *Schismus* persist and have diversified because they have adopted an annual reproductive strategy, produce a lot of small, compact diaspores and can thereby rely on stochastic burial. Exploitation of this new niche has removed the disadvantage of not having an awn. We have corroborated what Verboom et al. (2006) speculated, that under some circumstances having a hygroscopically active awn offers little benefit. Just as animals that have adapted to life in dark caves lose their pigmentation and the ability to see (Culver 1982), birds that have escaped the constraints of predation lose the ability to fly (Roff 1994) or plants that have become holoparasitic lose their photosynthesising appendages (Kujit 1969), awns (and the active burial syndrome) are lost when they are no longer needed.

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Appendix I. Character states and callus length for each species. Species sampled in the molecular phylogeny are marked in bold.

Taxon	Lemma awn	Life history	Lemma indumentum	Callus indumentum	Min. callus length (mm)	Max callus length (mm)
Austroderia fulvida (Buchanan) N.P.Barker & H.P.Linder	**awn**	**perennial**	**villous**	**villous**	**0.7**	**1.2**
Austroderia richardii (Endl.) N.P.Barker & H.P.Linder	**awn**	**perennial**	**villous**	**villous**	**1**	**1.5**
Austroderia splendens (Connor) N.P.Barker & H.P.Linder	**awn**	**perennial**	**villous**	**villous**	**1**	**1.5**
Austroderia toetoe (Zotov) N.P.Barker & H.P.Linder	**awn**	**perennial**	**villous**	**villous**	**0.7**	**1**
Austroderia turbaria (Connor) N.P.Barker & H.P.Linder	**awn**	**perennial**	**villous**	**villous**	**0.5**	**1**
Capeochloa arundinacea (Bergius) N.P.Barker & H.P.Linder	**awn**	**perennial**	**villous**	**villous**	**0.5**	**0.75**
Capeochloa cincta (Nees) N.P.Barker & H.P.Linder ssp. cincta	**awn**	**perennial**	**villous**	**villous**	**0.8**	**1**
Capeochloa setacea (N.P.Barker) N.P.Barker & H.P.Linder	**awn**	**perennial**	**villous**	**villous**	-	-
Chaetobromus involucratus Nees ssp. involucratus	**awn**	**perennial**	**villous**	**villous**	**1**	**1.8**
Chionochloa acicularis Zotov	**awn**	**perennial**	**villous**	**villous**	**0.7**	**1**
Chionochloa antarctica (Hook.f.) Zotov	**awn**	**perennial**	**villous**	**villous**	**0.75**	**1**
Chionochloa australis (Buchanan) Zotov	**awn**	**perennial**	**villous**	**villous**	**1**	**1**
Chionochloa beddiei Zotov	**awn**	**perennial**	**villous**	**villous**	**1**	**1**
Chionochloa bromoides (Hook.f.) Zotov	awn	perennial	villous	villous	1	1.5
Chionochloa cheesemanii (Hack. ex Cheeseman) Zotov	**awn**	**perennial**	**villous**	**villous**	**1.25**	**1.5**
Chionochloa conspicua (G.Forst.) Zotov ssp. conspicua	**awn**	**perennial**	**villous**	**villous**	**1**	**1.3**
Chionochloa crassiuscula (Kirk) Zotov ssp. crassiuscula Connor	**awn**	**perennial**	**villous**	**villous**	**0.9**	**1**
Chionochloa defracta Connor	**awn**	**perennial**	**villous**	**villous**	**1**	**1.25**
Chionochloa flavescens Zotov ssp. flavescens Connor	**awn**	**perennial**	**villous**	**villous**	**0.8**	**1**
Chionochloa flavicans Zotov	**awn**	**perennial**	**villous**	**villous**	**1.5**	**1.5**
Chionochloa frigida (Vickery) Conert	**awn**	**perennial**	**villous**	**villous**	**1**	**1.4**
Chionochloa howensis Jacobs	awn	perennial	villous	villous	-	-
Chionochloa juncea Zotov	**awn**	**perennial**	**villous**	**villous**	**1**	**1.1**
Chionochloa lanea Connor	**awn**	**perennial**	**villous**	**villous**	**0.8**	**1**
Chionochloa macra Zotov	**awn**	**perennial**	**villous**	**villous**	**0.6**	**0.8**
Chionochloa nivifera Connor & K.M.Lloyd	**awn**	**perennial**	**villous**	**villous**	**0.6**	**1**
Chionochloa oreophila (Petrie) Zotov	**awn**	**perennial**	**villous**	**villous**	**0.7**	**0.7**
Chionochloa ovata (Buchanan) Zotov	**awn**	**perennial**	**villous**	**villous**	**1**	**1**
Chionochloa pallens Zotov ssp. pallens Connor	**awn**	**perennial**	**villous**	**villous**	**1**	**1.5**
Chionochloa rigida (Raoul) Zotov ssp. amara Connor	**awn**	**perennial**	**villous**	**villous**	**1.3**	**1.3**
Chionochloa rubra Zotov ssp. rubra Connor var. rubra Connor	**awn**	**perennial**	**villous**	**villous**	**1**	**1**
Chionochloa spiralis Zotov	**awn**	**perennial**	**villous**	**villous**	**0.5**	**0.5**
Chionochloa teretifolia (Petrie) Zotov	**awn**	**perennial**	**villous**	**villous**	**0.75**	**1**
Chionochloa vireta Connor	**awn**	**perennial**	**villous**	**villous**	**0.8**	**1**
Cortaderia araucana Stapf	**awn**	**perennial**	**villous**	**villous**	**0.75**	**0.75**
Cortaderia atacamensis (Phil.) Pilg.	absent	perennial	villous	villous	0.5	0.6
Cortaderia bifida Pilg.	**awn**	**perennial**	**villous**	**villous**	**1**	**1**
Cortaderia boliviensis Lyle	**awn**	**perennial**	**villous**	**villous**	**0.5**	**0.5**
Cortaderia columbiana (Pilg.) Pilg.	**awn**	**perennial**	**villous**	**villous**	**0.75**	**0.9**
Cortaderia hapalotricha (Pilg.) Conert	**awn**	**perennial**	**villous**	**villous**	**0.9**	**1**
Cortaderia hieronymi (Kuntze) N.P.Barker & H.P.Linder	**awn**	**perennial**	**villous**	**villous**	**0.5**	**0.75**
Cortaderia jubata (Lem.) Stapf	**absent**	**perennial**	**villous**	**villous**	**0.75**	**1**
Cortaderia modesta (Doell) Hack	awn	perennial	villous	villous	0.7	0.9
Cortaderia nitida (Kunth) Pilg.	**awn**	**perennial**	**villous**	**villous**	**0.75**	**1.25**
Cortaderia peruviana (Hitchc.) N.P.Barker & H.P.Linder	**awn**	**perennial**	**villous**	**villous**	**1**	**1**
Cortaderia pilosa (D'Urv.) Hack. var. minima (Conert) Nicora	**awn**	**perennial**	**villous**	**villous**	**0.6**	**1**
Cortaderia planifolia Swallen	awn	perennial	villous	villous	-	-
Cortaderia roraimensis (N.E.Br.) Pilg.	awn	perennial	villous	villous	0.5	1
Cortaderia rudiuscula Stapf	**awn**	**perennial**	**villous**	**villous**	**0.5**	**0.75**
Cortaderia selloana (Schult.) Asch. & Graebn.	**awn**	**perennial**	**villous**	**villous**	**0.75**	**1**
Cortaderia sericantha (Steud.) Hitchc.	**awn**	**perennial**	**villous**	**villous**	**0.7**	**1**
Cortaderia speciosa (Nees) Stapf	absent	perennial	villous	villous	0.5	0.75
Cortaderia vaginata Swallen	awn	perennial	glabrous	villous	0.5	0.5
Danthonia alpina Vest	**awn**	**perennial**	**villous**	**villous**	**0.8**	**1**
Danthonia annablaea P.M.Peterson & Rugolo	**awn**	**perennial**	**villous**	**villous**	**0.6**	**0.7**
Danthonia araucana Phil.	**awn**	**perennial**	**villous**	**villous**	**0.5**	**1**
Danthonia boliviensis Renvoize	awn	perennial	villous	villous	-	-
Danthonia breviseta Hack.	awn	perennial	villous	villous	0.8	1
Danthonia californica Bol. var. californica	**awn**	**perennial**	**villous**	**villous**	**0.6**	**1**
Danthonia chaseana Conert	awn	perennial	villous	villous	0.4	0.5
Danthonia chiapasensis Davidse	awn	perennial	villous	villous	0.7	0.8
Danthonia chilensis E.Desv. & Gay var. chilensis	**awn**	**perennial**	**villous**	**villous**	**1**	**1**
Danthonia cirrata Hack. & Arechav.	awn	perennial	villous	villous	0.8	0.8
Danthonia compressa Austin	**awn**	**perennial**	**villous**	**villous**	**0.5**	**0.5**
Danthonia decumbens (L.) D.C.	**absent**	**perennial**	**villous**	**villous**	**0.5**	**0.5**
Danthonia domingensis Hack. & Pilg.	**awn**	**perennial**	**villous**	**villous**	**1**	**1.5**
Danthonia holm-nielsenii S.Laegaard	awn	perennial	villous	villous	0.8	0.8
Danthonia intermedia Vasey ssp. intermedia	**awn**	**perennial**	**villous**	**villous**	**0.8**	**1**
Danthonia malacantha (Steud.) Pilg.	**awn**	**perennial**	**villous**	**villous**	**0.7**	**0.8**
Danthonia melanathera (Hack.) Bernardello	awn	perennial	villous	villous	0.9	1.2
Danthonia montevidensis Hack. & Arechav.	awn	perennial	villous	villous	1	1
Danthonia parryi Scribn.	**awn**	**perennial**	**villous**	**villous**	**1.2**	**1.3**
Danthonia rhizomata Swallen	awn	perennial	villous	villous	1.7	1.7
Danthonia rugoloana Sulekic	awn	perennial	villous	villous	1	2.5
Danthonia secundiflora J.Presl & C.Presl ssp. secundiflora	**awn**	**perennial**	**villous**	**villous**	**0.9**	**1**
Danthonia sericea Nutt.	**awn**	**perennial**	**villous**	**villous**	**0.6**	**0.7**
Danthonia spicata (L.) P.Beauv.	**awn**	**perennial**	**villous**	**villous**	**0.5**	**0.5**
Danthonia unispicata (Thurb.) Munro ex Macoun	**awn**	**perennial**	**villous**	**villous**	**0.6**	**0.8**
Geochloa decora (Nees) N.P.Barker & H.P.Linder	**awn**	**perennial**	**villous**	**villous**	**1**	**1.5**
Geochloa lupulina (Thunb.) N.P.Barker & H.P.Linder	**awn**	**perennial**	**villous**	**villous**	**0.75**	**0.75**
Geochloa rufa (Nees) N.P.Barker & H.P.Linder	**awn**	**perennial**	**villous**	**villous**	-	-
Guineochloa archboldii (Hitchc.) Pirie & H.P.Linder	**awn**	**perennial**	**villous**	**villous**	**0.6**	**1.2**
Merxmuellera ambalavaoensis (A.Camus) Conert	awn	perennial	villous	villous	0.7	1.4
Merxmuellera davyi (C.E.Hubb.) Conert	**awn**	**perennial**	**villous**	**villous**	**0.8**	**1**

Appendix I. Character states and callus length for each species. Species sampled in the molecular phylogeny are marked in bold.

Merxmuellera drakensbergensis (Schweick.) Conert	**awn**	**perennial**	**villous**	**villous**	**0.7**	**0.9**
Merxmuellera grandiflora (Hochst) H.P.Linder	awn	perennial	villous	villous	1	1.2
Merxmuellera macowanii (Stapf) Conert	**awn**	**perennial**	**villous**	**villous**	**1**	**1**
Merxmuellera stereophylla (J.G.Anders.) Conert	**awn**	**perennial**	**villous**	**villous**	**0.6**	**0.7**
Merxmuellera tsaratananensis (A.Camus) Conert	awn	perennial	villous	villous	0.7	1.1
Notochloe microdon (Bentham) Domin	**absent**	**perennial**	**glabrous**	**villous**	**0.4**	**0.5**
Pentameris acinosa (Stapf) Galley & H.P.Linder	**awn**	**perennial**	**villous**	**villous**	**0.5**	**0.5**
Pentameris airoides Nees ssp. airoides	**awn**	**annual**	**villous**	**villous**	**0.1**	**0.1**
Pentameris alticola (H.P.Linder) Halley & H.P.Linder	**awn**	**perennial**	**villous**	**villous**	-	-
Pentameris ampla (Nees) Galley & H.P.Linder	**absent**	**perennial**	**villous**	**villous**	-	-
Pentameris andringitrensis (A.Camus) Galley & H.P.Linder	**awn**	**perennial**	**villous**	**villous**	-	-
Pentameris argentea (Stapf) Galley & H.P.Linder	**awn**	**perennial**	**glabrous**	**villous**	-	-
Pentameris aristidoides (Thunb.) Galley & H.P.Linder	**awn**	**perennial**	**villous**	**villous**	**1**	**1.5**
Pentameris aristifolia (Schweick.) Galley & H.P.Linder	**awn**	**annual**	**villous**	**villous**	-	-
Pentameris aspera (Thunb.) Galley & H.P.Linder	**awn**	**perennial**	**villous**	**villous**	-	-
Pentameris aurea (Steud.) Galley & H.P.Linder ssp. aurea	**absent**	**perennial**	**villous**	**villous**	-	-
Pentameris bachmannii (McClean) Galley & H.P.Linder	awn	perennial	villous	villous	-	-
Pentameris barbata (Nees) Steud. ssp. barbata	**awn**	**perennial**	**villous**	**villous**	-	-
Pentameris basutorum (Stapf) Galley & H.P.Linder	**awn**	**perennial**	**villous**	**villous**	-	-
Pentameris borussica (K. Schum) Galley & H.P.Linder	**awn**	**perennial**	**villous**	**villous**	-	-
Pentameris calcicola (H.P.Linder) Galley & H.P.Linder var. calcicola	**awn**	**perennial**	**villous**	**villous**	-	-
Pentameris capensis (Nees) Galley & H.P.Linder	**awn**	**perennial**	**villous**	**villous**	-	-
Pentameris capillaris (Thunb.) Galley & H.P.Linder	**absent**	**annual**	**glabrous**	**villous**	-	-
Pentameris caulescens (H.P.Linder) Galley & H.P.Linder	**awn**	**perennial**	**glabrous**	**villous**	-	-
Pentameris chippindalliae (H.P.Linder) Galley & H.P.Linder	**awn**	**perennial**	**villous**	**villous**	-	-
Pentameris chrysurus (K. Schum.) Galley & H.P.Linder	awn	perennial	villous	villous	0.25	0.25
Pentameris cirrhulosa (Nees) Steud.	**awn**	**perennial**	**villous**	**villous**	-	-
Pentameris clavata (Galley) Galley & H.P.Linder	**absent**	**perennial**	**villous**	**villous**	-	-
Pentameris colorata (Steud.) Galley & H.P.Linder	**awn**	**perennial**	**villous**	**villous**	**0.8**	**0.8**
Pentameris curvifolia (Schrad.) Steud.	**awn**	**perennial**	**villous**	**villous**	**0.3**	**0.3**
Pentameris densifolia (Nees) Galley & H.P.Linder	**awn**	**perennial**	**villous**	**villous**	-	-
Pentameris dentatum (L.f.) Galley & H.P.Linder	**absent**	**annual**	**villous**	**glabrous**	-	-
Pentameris distichophylla (Lehm.) Nees	**awn**	**perennial**	**villous**	**villous**	-	-
Pentameris dolichochaeta (S.M.Phillips) Galley & H.P.Linder	awn	perennial	villous	villous	-	-
Pentameris ecklonii (Nees) Galley & H.P.Linder	**absent**	**annual**	**villous**	**glabrous**	-	-
Pentameris elegans (Nees) Steud.	**awn**	**perennial**	**villous**	**villous**	-	-
Pentameris ellisii Linder, sp. nov	awn	perennial	villous	villous	0.1	0.3
Pentameris eriostoma (Nees) Steud.	**awn**	**perennial**	**villous**	**villous**	-	-
Pentameris exserta (H.P.Linder) Galley & H.P.Linder	**awn**	**perennial**	**villous**	**villous**	-	-
Pentameris galpinii (Stapf) Galley & H.P.Linder	**absent**	**perennial**	**villous**	**villous**	-	-
Pentameris glacialis N.P.Barker	**awn**	**perennial**	**villous**	**villous**	-	-
Pentameris glandulosa (Schrad.) Steud.	**awn**	**perennial**	**villous**	**villous**	-	-
Pentameris heptameris (Nees) Steud.	**awn**	**perennial**	**villous**	**villous**	-	-
Pentameris hirtiglumis N.P.Barker	**awn**	**perennial**	**villous**	**villous**	-	-
Pentameris holciformis (Nees) Galley & H.P.Linder	awn	perennial	villous	villous	-	-
Pentameris horrida (Galley) Galley & H.P.Linder	**awn**	**perennial**	**villous**	**villous**	**0.5**	**0.5**
Pentameris humbertii (A.Camus) Galley & H.P.Linder	awn	perennial	villous	villous	-	-
Pentameris insularis (Hemsl.) Galley & H.P.Linder	**awn**	**perennial**	**villous**	**villous**	-	-
Pentameris juncifolia (Stapf) Galley & H.P.Linder	**awn**	**perennial**	**villous**	**villous**	-	-
Pentameris lima (Nees) Steud.	**awn**	**perennial**	**villous**	**villous**	-	-
Pentameris longiglumis (Nees) Steud. ssp. longiglumis	**awn**	**perennial**	**villous**	**villous**	-	-
Pentameris longipes (Stapf) Galley & H.P.Linder	**awn**	**perennial**	**villous**	**villous**	-	-
Pentameris macrocalycina (Steud.) Schweick.	**awn**	**perennial**	**villous**	**villous**	-	-
Pentameris malouinensis (Steud.) Galley & H.P.Linder	**absent**	**perennial**	**villous**	**villous**	-	-
Pentameris microphylla (Nees) Galley & H.P.Linder	**absent**	**perennial**	**villous**	**villous**	-	-
Pentameris minor (Ballard & C.E.Hubb) Galley & H.P.Linder	**awn**	**perennial**	**villous**	**villous**	-	-
Pentameris montana (H.P.Linder) Galley & H.P.Linder	**awn**	**perennial**	**villous**	**villous**	-	-
Pentameris natalensis (Stapf) Galley & H.P.Linder	**awn**	**perennial**	**villous**	**villous**	**0.2**	**0.2**
Pentameris obtusifolia (Hochst.) Schweick.	**awn**	**perennial**	**villous**	**villous**	-	-
Pentameris oreodoxa (Schweick.) Galley & H.P.Linder	**awn**	**perennial**	**villous**	**villous**	-	-
Pentameris oreophila N.P.Barker	**awn**	**perennial**	**villous**	**villous**	-	-
Pentameris pallescens (Schrad.) Steud.	**awn**	**perennial**	**villous**	**villous**	-	-
Pentameris pallida (Thunb.) Galley & H.P.Linder form B	**awn**	**perennial**	**villous**	**villous**	**0.2**	**0.2**
Pentameris papillosa (Steud.) Steud.	**awn**	**perennial**	**villous**	**villous**	**0.4**	**0.4**
Pentameris patula (Nees) Steud.	**awn**	**annual**	**villous**	**villous**	-	-
Pentameris pholiuroides (Stapf) Galley & H.P.Linder	**absent**	**annual**	**glabrous**	**glabrous**	**0.2**	**0.2**
Pentameris pictigluma (Hochst.) Galley & H.P.Linder var. gracilis (S.M.Phillips) Galley & H.P.Linder	**awn**	**perennial**	**villous**	**villous**	-	-
Pentameris praecox (H.P. Linder) Galley & H.P.Linder	**awn**	**perennial**	**villous**	**villous**	-	-
Pentameris pseudopallescens (H.P. Linder) Galley & H.P.Linder	**awn**	**perennial**	**villous**	**villous**	**0.5**	**0.8**
Pentameris pungens (H.P. Linder) Galley & H.P.Linder	**awn**	**perennial**	**villous**	**villous**	**0.7**	**0.7**
Pentameris pusilla (Nees) Galley & H.P.Linder	**absent**	**perennial**	**villous**	**villous**	-	-
Pentameris pyrophila (H.P.Linder) Galley & H.P.Linder	**awn**	**perennial**	**villous**	**villous**	**0.5**	**0.7**
Pentameris reflexa (H.P.Linder) Galley & H.P.Linder	**absent**	**perennial**	**villous**	**villous**	-	-
Pentameris rigidissima (H.P.Linder) Galley & H.P.Linder	**awn**	**perennial**	**villous**	**villous**	**0.3**	**0.3**
Pentameris rosea (H.P.Linder) Galley & H.P.Linder ssp. purpurascens (H.P.Linder) Galley & H.P.Linder	**awn**	**perennial**	**villous**	**villous**	-	-
Pentameris rupestris (Nees) Steud.	**awn**	**perennial**	**villous**	**villous**	-	-
Pentameris scandens (H.P.Linder) Galley & H.P.Linder	**awn**	**perennial**	**villous**	**villous**	-	-
Pentameris setifolia (Thunb.) Galley & H.P.Linder	**absent**	**perennial**	**villous**	**villous**	-	-
Pentameris swartbergensis N.P.Barker	**awn**	**perennial**	**villous**	**villous**	-	-
Pentameris thuarii P.Beauv.	**awn**	**perennial**	**villous**	**villous**	-	-
Pentameris tomentella (Stapf) Galley & H.P.Linder	**awn**	**perennial**	**villous**	**villous**	-	-
Pentameris tortuosa (Trin.) Nees	**awn**	**perennial**	**villous**	**villous**	-	-
Pentameris trifida (Galley) Galley & H.P.Linder	**awn**	**perennial**	**villous**	**villous**	**0.8**	**0.8**
Pentameris triseta (Thunb.) Galley & H.P.Linder	**awn**	**annual**	**glabrous**	**villous**	-	-
Pentameris trisetoides (Hochst. ex Steud.) Galley & H.P.Linder	awn	perennial	villous	villous	0.1	0.1

Appendix I. Character states and callus length for each species. Species sampled in the molecular phylogeny are marked in bold.

Pentameris tysonii (Stapf) Galley & H.P.Linder	**awn**	**perennial**	**villous**	**villous**	**-**	**-**
Pentameris uniflora N.P.Barker	awn	perennial	villous	villous	-	-
Pentameris velutina (H.P.Linder) Galley & H.P.Linder	**awn**	**perennial**	**villous**	**villous**	**-**	**-**
Pentameris veneta (H.P.Linder) Galley & H.P.Linder	**awn**	**perennial**	**villous**	**villous**	**-**	**-**
Pentameris viscidula (Nees) Steud.	**awn**	**perennial**	**glabrous**	**villous**	**-**	**-**
Plinthanthesis paradoxa (R.Br.) S.T. Blake	**absent**	**perennial**	**villous**	**glabrous**	**0.2**	**0.4**
Plinthanthesis rodwayi (C.E. Hubb.) S.T. Blake	**absent**	**perennial**	**villous**	**villous**	**0.2**	**0.5**
Plinthanthesis urvillei Steud.	**awn**	**perennial**	**villous**	**villous**	**0.1**	**0.3**
Pseudopentameris brachyphylla (Stapf) Conert	**awn**	**perennial**	**villous**	**villous**	**2.5**	**2.5**
Pseudopentameris caespitosa N.P.Barker	**awn**	**perennial**	**glabrous**	**villous**	**4**	**4**
Pseudopentameris macrantha (Schrad.) Conert	**awn**	**perennial**	**villous**	**villous**	**3**	**4**
Rytidosperma acerosum (Vickery) Connor & Edgar	**awn**	**perennial**	**villous**	**villous**	**0.7**	**1**
Rytidosperma alpicolum (Vickery) Connor & Edgar	**awn**	**perennial**	**villous**	**villous**	**0.3**	**0.8**
Rytidosperma auriculatum (J.M.Black) Connor & Edgar	**awn**	**perennial**	**villous**	**villous**	**0.51**	**0.9**
Rytidosperma australe (Petrie) Connor & Edgar.	**absent**	**perennial**	**glabrous**	**glabrous**	**0.01**	**0.2**
Rytidosperma biannulare (Zotov) Connor & Edgar	awn	perennial	villous	villous	0.5	0.7
Rytidosperma bipartitum (Kunth) A.M.Humphreys & H.P.Linder	**awn**	**perennial**	**villous**	**villous**	**0.6**	**1.2**
Rytidosperma bonthainicum (Jansen) A.M.Humphreys & H.P.Linder	awn	perennial	villous	villous	0.6	0.7
Rytidosperma buchananii (Hook.f.) Connor & Edgar	**awn**	**perennial**	**villous**	**villous**	**0.4**	**0.5**
Rytidosperma caespitosum (Gaudich.) Connor & Edgar	**awn**	**perennial**	**villous**	**villous**	**0.6**	**1**
Rytidosperma carphoides (Vickery) Connor & Edgar	**awn**	**perennial**	**villous**	**villous**	**0.5**	**1**
Rytidosperma clavatum (Zotov) Connor & Edgar	**awn**	**perennial**	**villous**	**villous**	**0.6**	**1**
Rytidosperma clelandii (Vickery) Connor & Edgar	**awn**	**perennial**	**villous**	**villous**	**0.8**	**1**
Rytidosperma corinum Connor & Edgar	awn	perennial	villous	villous	0.4	0.5
Rytidosperma craigii (Veldkamp) H.P.Linder	awn	perennial	villous	villous	0.2	0.4
Rytidosperma dendeniwae (Veldkamp) H.P.Linder	awn	perennial	villous	villous	-	-
Rytidosperma diemenicum (D.I. Morris) A.M.Humphreys & H.P.Linder	awn	perennial	villous	villous	0.4	0.8
Rytidosperma dimidiatum (Vickery) Connor & Edgar	**awn**	**perennial**	**villous**	**villous**	**0.45**	**0.7**
Rytidosperma duttonianum (Cashmore) Connor & Edgar	**awn**	**perennial**	**villous**	**villous**	**0.5**	**1**
Rytidosperma erianthum (Lindl.) Connor & Edgar	**awn**	**perennial**	**villous**	**villous**	**0.8**	**1.2**
Rytidosperma exigua (Kirk) H.P.Linder	**absent**	**perennial**	**villous**	**glabrous**	**0.3**	**0.5**
Rytidosperma fortunae-hibernae (Renv.) Connor & Edgar	awn	perennial	villous	villous	0.3	0.4
Rytidosperma fulvum (Vickery) A.M.Humphreys & H.P.Linder	**awn**	**perennial**	**villous**	**villous**	**0.6**	**1.3**
Rytidosperma geniculatum (J.M. Black) Connor & Edgar	**awn**	**perennial**	**villous**	**villous**	**0.6**	**1**
Rytidosperma gracile (Hook.f.) Connor & Edgar	**awn**	**perennial**	**villous**	**villous**	**0.3**	**0.5**
Rytidosperma horrens Connor et Molloy	awn	perennial	villous	villous	0.25	0.25
Rytidosperma indutum (Vickery) Connor & Edgar	**awn**	**perennial**	**villous**	**villous**	**0.6**	**1.5**
Rytidosperma javanicum (Ohwi ex Veldkamp) H.P.Linder	awn	perennial	villous	villous	-	-
Rytidosperma laeve (Vickery) Connor & Edgar	**awn**	**perennial**	**villous**	**villous**	**0.7**	**1.2**
Rytidosperma lechleri Steud.	**awn**	**perennial**	**villous**	**villous**	**0.3**	**0.5**
Rytidosperma lepidopodum (Walsh) A.M.Humphreys & H.P.Linder	**awn**	**perennial**	**villous**	**villous**	**0.6**	**1.2**
Rytidosperma longifolium (R.Br.) Connor & Edgar	**awn**	**perennial**	**villous**	**villous**	**0.2**	**0.7**
Rytidosperma maculatum (Zotov) Connor & Edgar	**awn**	**perennial**	**villous**	**villous**	**0.4**	**0.4**
Rytidosperma mamberamense (Jansen) Connor & Edgar	awn	perennial	villous	villous	-	-
Rytidosperma merum Connor & Edgar	**awn**	**perennial**	**villous**	**villous**	**0.6**	**1**
Rytidosperma monticolum (Vickery) Connor & Edgar	**awn**	**perennial**	**villous**	**villous**	**0.5**	**1**
Rytidosperma montis-wilhelmii (Veldkamp & Fortuin) H.P.Linder	awn	perennial	villous	villous	0.5	0.6
Rytidosperma nardifolium (Veldkamp) H.P.Linder	awn	perennial	villous	villous	0.5	0.5
Rytidosperma nigricans (Petrie) Connor & Edgar	awn	perennial	villous	villous	0.2	0.5
Rytidosperma nitens (D.I.Morris) H.P.Linder	**awn**	**perennial**	**glabrous**	**villous**	**0.3**	**0.6**
Rytidosperma nivicolum (Vickery) Connor & Edgar	**awn**	**perennial**	**villous**	**villous**	**0.4**	**0.5**
Rytidosperma nudiflorum (P.F.Morris) Connor & Edgar	**awn**	**perennial**	**villous**	**villous**	**0.3**	**0.6**
Rytidosperma nudum (Hook.f.) Connor & Edgar	awn	perennial	villous	villous	0.3	0.35
Rytidosperma occidentale (Vickery) Connor & Edgar	**awn**	**perennial**	**villous**	**villous**	**1**	**1.6**
Rytidosperma oreoboloides (F. Muell.) H.P.Linder	**absent**	**perennial**	**villous**	**villous**	**0.1**	**0.2**
Rytidosperma oreophilum H.P.Linder & N.G.Walsh	**awn**	**perennial**	**villous**	**villous**	**0.7**	**1**
Rytidosperma pallidum (R.Br.) A.M.Humphreys & H.P.Linder	**awn**	**perennial**	**villous**	**villous**	**0.4**	**1.2**
Rytidosperma paschalis (Pilg.) Baeza	**awn**	**perennial**	**villous**	**villous**	**0.6**	**1**
Rytidosperma pauciflorum (R.Br.) Connor & Edgar	**awn**	**perennial**	**villous**	**villous**	**0.2**	**0.3**
Rytidosperma penicillatum (Labill.) Connor & Edgar	**awn**	**perennial**	**villous**	**villous**	**0.5**	**1.3**
Rytidosperma petrosum Connor & Edgar	**awn**	**perennial**	**villous**	**villous**	**0.7**	**1**
Rytidosperma pictum (Nees & Meyen) Nicora var. pictum Nicora	**awn**	**perennial**	**villous**	**villous**	**0.4**	**0.5**
Rytidosperma pilosum (R.Br.) Connor & Edgar	**awn**	**perennial**	**villous**	**villous**	**0.6**	**1**
Rytidosperma popinensis (D.I. Morris) A.M.Humphreys & H.P.Linder	**awn**	**perennial**	**villous**	**villous**	**1**	**1.2**
Rytidosperma pulchrum (Zotov) Connor & Edgar	**awn**	**perennial**	**villous**	**villous**	**0.2**	**0.4**
Rytidosperma pumilum (Kirk) Connor & Edgar	**absent**	**perennial**	**villous**	**glabrous**	**0.2**	**0.2**
Rytidosperma quirihuense M.Baeza	**awn**	**perennial**	**villous**	**villous**	**1**	**1.2**
Rytidosperma racemosum var. racemosum (R.Br.) Connor & Edgar	**awn**	**perennial**	**villous**	**villous**	**0.8**	**1.4**
Rytidosperma remotum (D.I.Morris) A.M.Humphreys & H.P.Linder	awn	perennial	villous	villous	0.5	0.9
Rytidosperma richardsonii (Cashmore) Connor & Edgar	**awn**	**perennial**	**villous**	**villous**	**1**	**1.2**
Rytidosperma semiannulare (Labill.) Connor & Edgar	**awn**	**perennial**	**villous**	**villous**	**0.3**	**0.6**
Rytidosperma setaceum (R.Br.) Connor & Edgar	**awn**	**perennial**	**villous**	**villous**	**0.4**	**1.1**
Rytidosperma setifolium (Hook.f.) Connor & Edgar	**awn**	**perennial**	**villous**	**villous**	**0.5**	**0.6**
Rytidosperma sorianoi Nicora	awn	perennial	villous	villous	0.3	0.5
Rytidosperma telmaticum Connor et Molloy	**absent**	**perennial**	**villous**	**villous**	**0.1**	**0.25**
Rytidosperma tenue (Petrie) Connor & Edgar	awn	perennial	villous	villous	0.2	0.3
Rytidosperma tenuius (Steud.) O.E.Erikss., A.Hansen & Sunding	**awn**	**perennial**	**villous**	**villous**	**0.8**	**1.3**
Rytidosperma thomsonii (Buchanan) Connor & Edgar	**awn**	**perennial**	**villous**	**villous**	**0.2**	**0.4**
Rytidosperma unarede (Raoul) A.M.Humphreys & H.P.Linder	**awn**	**perennial**	**villous**	**villous**	**1.8**	**1.8**
Rytidosperma vestitum (Pilg.) Connor & Edgar	awn	perennial	villous	villous	0.7	0.8
Rytidosperma vickeryae Gray & H.P.Linder, sp. nov.	**awn**	**perennial**	**villous**	**villous**	**0.4**	**0.5**
Rytidosperma violaceum (Desv.) Nicora	**awn**	**perennial**	**villous**	**villous**	**0.5**	**0.5**
Rytidosperma virescens (E.Desv.) Nicora var. virescens	**awn**	**perennial**	**villous**	**villous**	**0.7**	**0.7**
Rytidosperma viride (Zotov) Connor & Edgar	awn	perennial	villous	villous	0.5	0.5
Schismus arabicus Nees	**absent**	**annual**	**villous**	**villous**	**0.1**	**0.2**
Schismus barbatus (Loefl. ex L.) Thell.	**absent**	**annual**	**villous**	**villous**	**0.1**	**0.2**
Schismus inermis (Stapf) C.E. Hubbard	absent	perennial	villous	villous	0.3	0.3

Appendix I. Character states and callus length for each species. Species sampled in the molecular phylogeny are marked in bold.

Schismus scaberrimus Nees	**absent**	**perennial**	**villous**	**villous**	**0.25**	**0.3**
Schismus schismoides (Stapf ex Conert) H.P.Linder	**awn**	**annual**	**villous**	**villous**	**0.4**	**0.6**
Tenaxia aureocephala (J.G. Anderson) N.P.Barker & H.P.Linder	**awn**	**perennial**	**villous**	**villous**	**1.5**	**1.5**
Tenaxia cachemyriana (Jaub. & Spach) N.P.Barker & H.P.Linder	awn	perennial	villous	villous	0.3	0.7
Tenaxia cumminsii (Hook.f.) N.P.Barker & H.P.Linder	**awn**	**perennial**	**villous**	**villous**	**0.5**	**0.8**
Tenaxia disticha (Nees) N.P.Barker & H.P.Linder	**awn**	**perennial**	**villous**	**villous**	**0.5**	**1**
Tenaxia dura (Stapf) Conert, N.P.Barker & H.P.Linder	**awn**	**perennial**	**villous**	**villous**	**1.4**	**1.4**
Tenaxia guillarmodae (Conert) N.P.Barker & H.P.LInder	awn	perennial	villous	villous	0.8	1.2
Tenaxia stricta (Schrad.) N.P.Barker & H.P.Linder	**awn**	**perennial**	**villous**	**villous**	**0.75**	**1**
Tenaxia subulata (A.Rich.) N.P.Barker & H.P.Linder	**awn**	**perennial**	**villous**	**villous**	**0.9**	**1**
Tribolium acutiflorum (Nees) Renvoize	**absent**	**perennial**	**villous**	**glabrous**	**0.3**	**0.5**
Tribolium brachystachyum (Nees) Renvoize	**absent**	**perennial**	**villous**	**glabrous**	**0.2**	**0.2**
Tribolium ciliare (Stapf) Renvoize	**absent**	**annual**	**villous**	**glabrous**	**0.1**	**0.1**
Tribolium curva (Nees) Verboom & H.P.Linder	**awn**	**perennial**	**villous**	**villous**	**0.2**	**0.3**
Tribolium echinatum (Thunb.) Renvoize	**absent**	**annual**	**villous**	**glabrous**	**0.2**	**0.2**
Tribolium hispidum (Thunb.) Renvoize	**absent**	**perennial**	**villous**	**glabrous**	**0.1**	**0.2**
Tribolium obliterum (Hemsl.) Renvoize	**absent**	**perennial**	**villous**	**glabrous**	**0.2**	**0.3**
Tribolium obtusifolium (Nees) Renvoize	**absent**	**perennial**	**villous**	**glabrous**	**0.2**	**0.3**
Tribolium pleuropogon (Stapf) Verboom & H.P.Linder	**awn**	**perennial**	**villous**	**villous**	**0.1**	**0.1**
Tribolium purpurea (L.f.) Verboom & H.P.Linder	awn	perennial	villous	villous	0.8	0.8
Tribolium pusillum (Nees) H.P.Linder & Davidse	**awn**	**annual**	**villous**	**glabrous**	-	-
Tribolium tenella (Nees) Verboom & H.P.Linder	**awn**	**annual**	**villous**	**villous**	**0.3**	**0.3**
Tribolium uniolae (L.f.) Renvoize	**absent**	**perennial**	**villous**	**glabrous**	**0.3**	**0.5**
Tribolium utriculosum (Nees) Renvoize	**absent**	**annual**	**villous**	**glabrous**	**0.2**	**0.2**

Appendix II. Ancestral state reconstructions using parsimony, ML and rj-mcmc. (i) All taxa. (ii) Excluding *Schismus* and *Tribolium.*

(i) All taxa

Node number	Node name	p.p.	MRCA of	State (MP)	ML(1)	P(1) mean rjmcmc	age (min95%)	age (max95%)
1	**1**	1.0	Mer_davyi_NPB942 Mer_stereophylla_PM3 Mer_macowanii_NPB1008 Mer_drakensbergensis_PM4	0	0.09401	0.0448	5.85	16.65
2	**2**	1.0	Geo_decora_NPB11 Cap_cincta_NPB1160	0	0.13452	0.0639	16.88	20.73
3	**3**	1.0	Geo_decora_NPB1168 Ryt_quirihuense_MDP338	0	0.17596	0.0788	20.40	22.55
4	**4**	1.0	Pen_praecox_MDP490 Ryt_quirihuense_MDP338	0	0.34658	0.1820	19.75	22.11
5	**5**	1.0	Pen_praecox_MDP490 Pen_pictigluma_mannii_CG267_ITS	0	0.30755	0.1610	11.35	13.37
6	**6**	1.0	Chi_australis_OTA57584_ITS Ryt_quirihuense_MDP338	0	0.23318	0.1090	18.70	21.37
7	**7**	1.0	Pen_praecox_MDP490 Pen_thuarii_HPL5456 Pen_macrocalycina_GAV203	0	0.11032	0.0514	6.11	9.02
8	**8**	1.0	Pen_elegans_CG336 Pen_colorata_CG538 Pen_tortuosa_GAV250 Pen_alticola_CG377 Pen_rigidissima_G	0	0.12543	0.0585	4.10	7.20
9	**8b**	0.99	Pen_colorata_CG538 Pen_clavata_HPL6893 Pen_tortuosa_GAV250 Pen_rigidissima_GAV227	0	0.06454	0.0319	3.41	6.60
10	**8c**	0.91	Pen_alticola_CG377 Pen_colorata_CG538 Pen_clavata_HPL6893 Pen_tortuosa_GAV250	0	0.13063	0.0631	2.32	4.99
11	**9**	1.0	Pen_elegans_CG336 Pen_pictigluma_mannii_CG267_ITS Pen_alticola_CG377 Pen_basutorum_CG44 Pe	0	0.19175	0.0867	6.77	8.82
12	**10**	0.84	Pen_basutorum_CG44 Pen_basutorum_CG44_ITS Pen_andringitrensis_CG595 Pen_pusilla_GAV206 Pen	0	0.31195	0.1440	6.49	8.48
13	**11**	1.0	Pen_pusilla_GAV206 Pen_viscidula_HPL7787 Pen_exserta_CG51 Pen_ampla_GAV197 Pen_aurea_aurea_	0	0.73343	0.4300	5.48	7.11
14	**15**	1.0	Pen_aurea_aurea_HPL6813 Pen_aurea_pilosogluma_CG47	1	0.99664	0.9970	0.55	1.95
15	**16**	0.97	Pen_malouinensis_GAV218_ITS Pen_malouinensis_GAV218 Pen_pungens_CG333	0	0.24352	0.1140	3.76	5.78
16	**17**	0.99	Pen_scandens_CG334 Pen_caulescens_CG376 Pen_curvifolia_TvN52 Pen_acinosa_TvN1 Pen_horrida_Tv	0	0.26710	0.1220	2.96	4.85
17	**20**	0.87	Pen_horrida_TvN20_ITS Pen_malouinensis_GAV218_ITS	0	0.61216	0.4710	0.48	2.60
18	**21**	0.84	Pen_capensis_HPL6825 Pen_pyrophila_GAV229 Pen_argentea_GAV254 Pen_malouinensis_GAV218 Pen_	0	0.28738	0.1450	2.61	4.62
19	**22**	0.95	Pen_argentea_GAV254 Pen_pyrophila_GAV229	0	0.40418	0.2160	2.13	4.15
20	**23**	0.85	Pen_malouinensis_GAV218 Pen_pyrophila_GAV229	0	0.62039	0.4120	1.83	3.72
21	**24**	1.0	Pen_pungens_CG333 Pen_pyrophila_GAV229 Pen_eriostoma_P6	0	0.11530	0.0557	1.39	3.07
22	**25**	1.0	Pen_dentatum_HPL5430 Pen_pictigluma_mannii_CG267_ITS	0	0.47254	0.2370	4.74	6.27
23	**26**	1.0	Pen_dentatum_HPL5430 Pen_velutina_CG389_ITS	0	0.63242	0.5170	3.98	5.65
24	**27**	1.0	Pen_dentatum_HPL5430 Pen_pholiuroides_HPL5402	1	0.96939	0.9800	1.17	2.61
25	**28**	1.0	Pen_rosea_purpurascens_CG378 Pen_horrida_TvN20 Pen_velutina_CG389_ITS Pen_pallescens_GAV216	0	0.10552	0.0528	2.00	3.47
26	**29**	1.0	Pen_trifida_CG577 Pen_velutina_CG389 Pen_triseta_HPL6962 Pen_densifolia_GAV225 Pen_calcicola_ca	0	0.30619	0.1400	4.31	5.82
27	**30**	0.94	Pen_densifolia_GAV225 Pen_pictigluma_mannii_CG267_ITS	0	0.39835	0.1860	3.77	5.15
28	**31**	1.0	Pen_calcicola_calci_CG338 Pen_pictigluma_mannii_CG267_ITS	0	0.55610	0.2480	3.04	4.28
29	**32**	1.0	Pen_calcicola_calci_CG338 Pen_densifolia_GAV225_ITS Pen_ecklonii_HPL6136 Pen_heptamera_CG356	0	0.22798	0.1140	2.35	3.54
30	**35 *new**		Pen_ecklonii_HPL6136 Pen_reflexa_CG324	0	0.48771	0.4150	0.11	0.86
31	**36**	0.86	Pen_cirrhulosa_CG548 Pen_papillosa_GAV209	0	0.06360	0.0312	0.56	1.59
32	**37**	1.0	Pen_chippindalliae_CG96_ITS Pen_reflexa_CG324_ITS Pen_natalensisSA_CG95 Pen_setifolia_CG45 Pen	0	0.73000	0.3450	2.54	3.62
33	**38**	0.96	Pen_glandulosa_HPL6814 Pen_setifolia_CG45 Pen_oreodoxa_CG32	0	0.31657	0.1900	0.63	2.27
34	**40**	1.0	Pen_capillaris_CG322 Pen_veneta_CG576 Pen_airoides_airoides_HPL6971 Pen_galpinii_CG42 Pen_lima_	0	0.49783	0.2690	1.57	2.56
35	**41**	1.0	Pen_capillaris_CG322 Pen_veneta_CG576	0	0.85256	0.7690	0.90	2.02
36	**42**	0.83	Pen_airoides_jugorum_CG81 Pen_airoides_airoides_HPL6971 Pen_galpinii_CG42 Pen_lima_HPL6972 P	0	0.16254	0.0694	1.12	2.18
37	**43**	0.98	Pen_airoides_airoides_HPL6971 Pen_insularis	0	0.06499	0.0323	0.35	1.43
38	**44**	0.93	Pen_airoides_airoides_HPL6971 Pen_insularis Pen_galpinii_CG42 Pen_lima_HPL6972	0	0.51577	0.2750	0.94	1.85
39	**46**	1.0	Pen_aristifolia_CG388 Pen_lima_HPL6972	0	0.10181	0.0465	0.18	0.58
40	**47**	1.0	Pen_borussicaE_HPL7661 Pen_pictigluma_mannii_CG267 Pen_pictigluma_mannii_CG267_ITS	0	0.01351	0.0081	0.64	1.29
41	**49**	1.0	Chi_australis_OTA57584_ITS Chi_defracta_OTA57937 Chi_juncea_OTA57967 Chi_rubra_OTA57960 Ch	0	0.11327	0.0505	13.02	19.34
42	**50**	1.0	Cha_involucratus_dreg_NPB978 Cor_columbiana_ML920 Not_microdon_AMH66_ITS Ten_disticha_NP	0	0.31394	0.1490	15.91	19.54
43	**51**	1.0	Cor_columbiana_ML920 Cor_jubata_ML1515	0	0.12150	0.0583	11.27	16.69
44	**52**	1.0	Cor_bifida_ML1497 Cor_sericantha_ML1128 Cor_boliviensis_ML672 Cor_hieronymi_OM3534 Cor_per	0	0.07328	0.0326	8.91	15.40
45	**53**	0.73	Cor_nitida_ML1434 Cor_jubata_ML1515	0	0.53412	0.3440	3.18	11.35
46	**55**	1.0	Cha_involucratus_dreg_NPB978 Pse_brachyphylla_NPB1669	0	0.38519	0.2100	8.28	11.26
47	**56**	1.0	Not_microdon_AMH66_ITS Ryt_quirihuense_MDP338	0	0.55700	0.3150	14.77	18.46
48	**57**	1.0	Not_microdon_AMH66_ITS Not_microdon_AMH66 Dan_decumbens_MDP312	0	0.57686	0.3660	13.67	17.88
49	**58**	1.0	Ten_disticha_NPB1002 Ten_subulata_HPL7669 Ryt_caespitosum_AMH92 Ryt_australe_AMH145 Ryt_qu	0	0.48453	0.2920	12.31	15.84
50	**59**	0.99	Not_microdon_AMH66_ITS Pli_paradoxa_HPL5638 Pli_rodwayi_MDP415 Pli_urvillei_MC4003	0.5	0.92817	0.8920	5.31	11.25
51	**60**	1.0	Not_microdon_AMH66_ITS Pli_paradoxa_HPL5638 Aus_splendens_G10872 Aus_toetoe_G5042	0	0.76099	0.6270	9.25	14.19
52	**61**	1.0	Aus_splendens_G10872 Aus_richardii_G3816 Aus_toetoe_G5042 Aus_turbaria_G17358 Aus_fulvida_G50	0	0.01269	0.0059	1.54	4.12
53	**62**	1.0	Cor_pilosa_MDP345 Cor_boliviensis_ITS Cor_hieronymi_ITS Not_microdon_AMH66 Cor_peruvianus_	0	0.16526	0.0642	10.04	15.55
54	**64 *new**		Cor_boliviensis_ITS Not_microdon_AMH66 Cor_jubata_ITS	0	0.50642	0.2320	8.88	14.72
55	**64b**	1.0	Cor_araucana_ITS Cor_jubata_ITS Cor_rudiuscula_ITS	0	0.69191	0.4910	0.79	4.03
56	**65**	0.85	Cor_bifida_ITS Cor_columbiana_ITS Cor_nitida_ITS Cor_sericantha_ITS	0	0.16388	0.0712	5.79	12.87
57	**66**	1.0	Gui_archboldii_JM115 Dan_parryi_CWM813 Dan_compressa_Radford44899 Dan_intermedia_Hermann	0	0.09240	0.0452	6.67	13.89
58	**67**	1.0	Dan_domingensis_AA373 Dan_parryi_CWM813 Dan_spicata_WDT95_30 Dan_unispicata_JTH52406 D	0	0.02620	0.0124	5.61	11.16
59	**68**	0.95	Dan_compressa_Radford44899 Dan_intermedia_Hermannsn Dan_decumbens_MDP312 Dan_chilensis_	0	0.06021	0.0312	4.63	10.46
60	**69**	0.97	Dan_alpina_MDP480 Dan_alpina_480_ITS Dan_decumbens_MDP312	0	0.43624	0.2640	1.47	5.35
61	**70**	1.0	Dan_secundiflora_ML1617 Dan_annableae_DMP1833 Dan_filifolia_MJM34 Dan_malacantha_MDP339	0	0.04884	0.0224	2.93	8.13
62	**71**	1.0	Ten_disticha_NPB1002 Ten_subulata_HPL7669	0	0.43417	0.2400	12.00	15.39
63	**72**	1.0	Sch_arabicus_Willissn Ryt_quirihuense_MDP338	0	0.67234	0.6100	8.52	11.85
64	**73**	1.0	Sch_schismoides_GAV562 Sch_barbatus_GAV503	0	0.81265	0.7660	5.01	7.32
65	**74**	1.0	Sch_arabicus_Willissn Sch_barbatus_GAV503 Sch_scaberrimus_GAV573	1	0.98016	0.9890	2.60	5.04
66	**75**	1.0	Tri_brachystachyum_GAV593 Tri_ciliare_GAV596_ITS Tri_obliterum_GAV598	eq	0.87935	0.9010	6.37	9.11
67	**76**	1.0	Tri_brachystachyum_GAV593 Tri_uniolae_GAV531	1	0.98611	0.9900	1.40	3.04
68	**77**	1.0	Tri_utriculosum_GAV568 Tri_obliterum_GAV598	eq	0.93687	0.8750	4.62	6.72
69	**78**	1.0	Tri_utriculosum_GAV568 Tri_ciliare_GAV596_ITS Tri_pusillum_GAV554_ITS Tri_hispidum_GAV532 Tr	0	0.99051	0.9940	2.82	4.68
70	**79**	0.99	Tri_tenella_GAV587 Tri_obtusifolium_GAV597 Tri_obliterum_GAV598	0, 20%; eq., 80%	0.76906	0.5700	4.31	6.30
71	**80**	0.99	Tri_ciliare_GAV596_ITS Tri_hispidum_GAV532 Tri_ciliare_GAV596 Tri_pusillum_GAV554_ITS Tri_echi	1, 80%; 0, 20%	0.98009	0.9810	2.52	4.22
72	**80b**	0.88	Tri_ciliare_GAV596 Tri_echinatum_GAV576	1, 80%; 0, 20%	0.99337	0.9950	0.38	2.35
73	**81**	1.0	Tri_pusillum_GAV554 Tri_acutiflorum_GAV504 Tri_obtusifolium_GAV597	0, 20%; eq., 80%	0.89327	0.8190	3.53	5.35
74	**82**	1.0	Tri_pusillum_GAV554 Tri_acutiflorum_GAV504	0, 20%; eq., 80%	0.82466	0.6960	2.43	3.80
75	**83**	1.0	Tri_acutiflorum_GAV504 Tri_obliterum_GAV598 Tri_pleuropogon_GAV628	0, 20%; eq., 80%	0.95187	0.9360	1.49	2.74
76	**84**	1.0	Tri_curva_GAV604 Tri_obtusifolium_GAV597	0, 20%; eq., 80%	0.89721	0.8240	1.06	2.82
77	**85**	1.0	Tri_brachystachyum_GAV593 Ryt_quirihuense_MDP338	0	0.59822	0.4830	7.14	10.25
78	**86**	1.0	Ryt_alpicolum_AMH102 Ryt_caespitosum_AMH92 Ryt_laeve_Wsn Ryt_pauciflorum_HPL5688 Ryt_bip	0	0.00545	0.0031	3.20	7.13
79	**87**	1.0	Ryt_alpicolum_AMH102 Ryt_tenuius_AMH70 Ryt_geniculatum_AMH39 Ryt_carphoides_HPL5568 Ryt_	0	0.00954	0.0038	2.57	6.20
80	**90**	1.0	Ryt_buchananii_AMH120 Ryt_maculatum_AMH117 Ryt_telmaticum_AMH151 Ryt_pumilum_NGW66	0	0.33869	0.1580	0.79	2.49
81	**91**	0.87	Ryt_telmaticum_AMH151 Ryt_pumilum_NGW6676 Ryt_thomsonii_AMH118	0, 20%; eq., 80%	0.90103	0.5810	0.61	1.83
82	**91b**	0.86	Ryt_pumilum_NGW6676 Ryt_thomsonii_AMH118	0, 20%; eq., 80%	0.63507	0.3750	0.34	1.33
83	**92**	1.0	Ryt_lechleri_CMB4256 Ryt_violaceum_MDP356 Ryt_australe_AMH145 Ryt_gracile_AMH148 Ryt_setifo	0	0.06433	0.0277	2.28	5.40
84	**93**	1.0	Ryt_australe_AMH145 Ryt_gracile_AMH148 Ryt_setifolium_AMH121	0	0.28254	0.1290	1.77	4.36
85	**94**	1.0	Ryt_australe_AMH145 Ryt_pulchrum_AMH143	0	0.87117	0.7500	1.03	3.08
86	**95**	1.0	Ryt_lechleri_CMB4256 Ryt_violaceum_MDP356	0	0.01289	0.0055	0.96	3.13
87	**96**	0.84	Ryt_gracile_AMH148 Ryt_setifolium_AMH121	0	0.06946	0.0310	1.60	4.23
88	**97**	1.0	Ryt_lechleri_CMB4256 Ryt_pulchrum_AMH143 Ryt_popinensis_AMH94 Ryt_quirihuense_MDP338	0	0.03735	0.0177	2.79	6.26
89	**98**	1.0	Ryt_popinensis_AMH94 Ryt_fulvum_AMH38 Ryt_exiguum_HPL5746 Ryt_quirihuense_MDP338	0	0.06746	0.0305	2.24	5.06
90	**99**	0.98	Ryt_popinensis_AMH94 Ryt_fulvum_AMH38 Ryt_pallidum_HPL5564	0	0.03344	0.0184	2.06	4.65
91	**100**	1.0	Ryt_exiguum_HPL5746 Ryt_vickeryae_MDP422 Ryt_oreoboloides_MWC8877 Ryt_nivicolum_MDP419	0	0.38543	0.1850	1.70	4.14
92	**101*new**		Ryt_exiguum_HPL5746 Ryt_oreoboloides_MWC8877	0	0.47609	0.2740	1.47	3.37
93	**103**	0.99	Ryt_merum_AMH125 Ryt_caespitosum_AMH25 Ryt_quirihuense_MDP338	0	0.01508	0.0079	1.42	3.31

Grey shading: ancestral state = '0'; yellow shading: ancestral state = '1'; no shading: ancestral state = ambiguous.

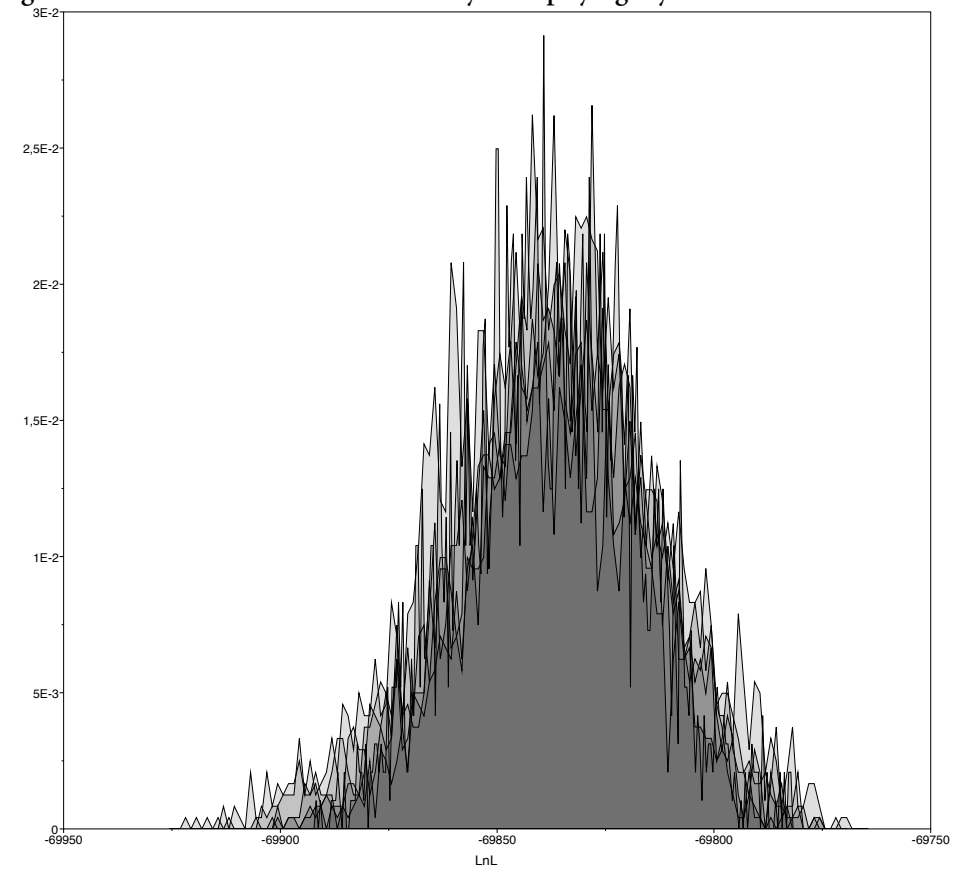
Appendix II. Ancestral state reconstructions using parsimony, ML and rj-mcmc. (i) All taxa. (ii) Excluding *Schismus* and *Tribolium.*

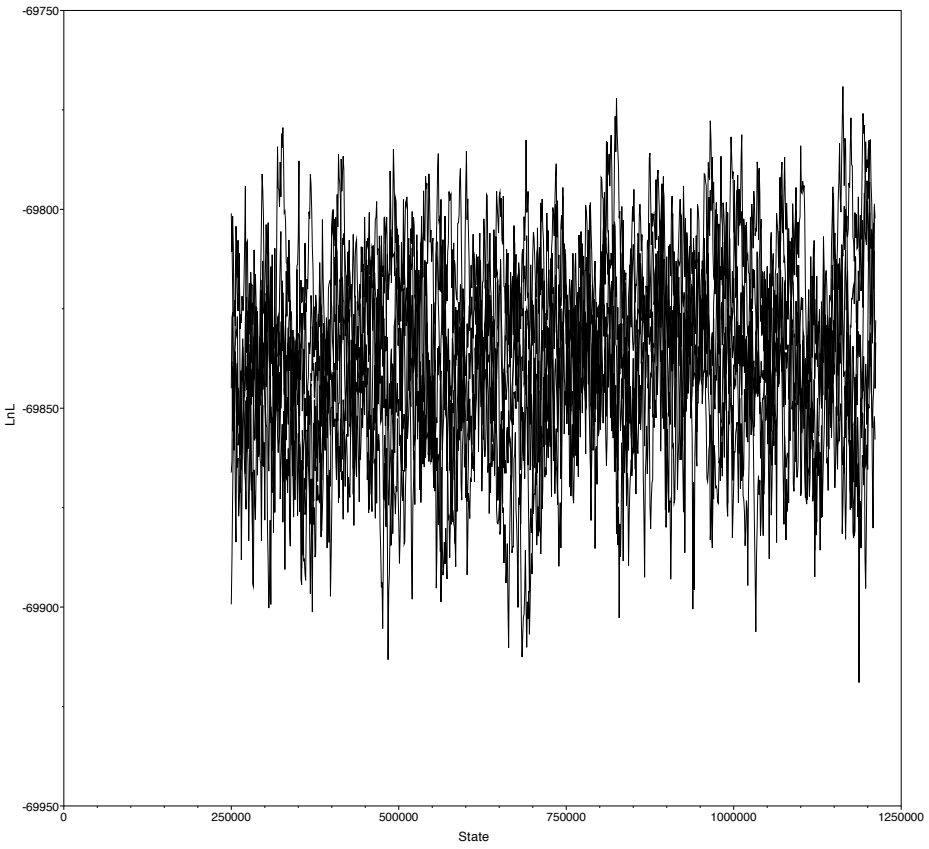
(ii) Excluding *Schismus* and *Tribolium*

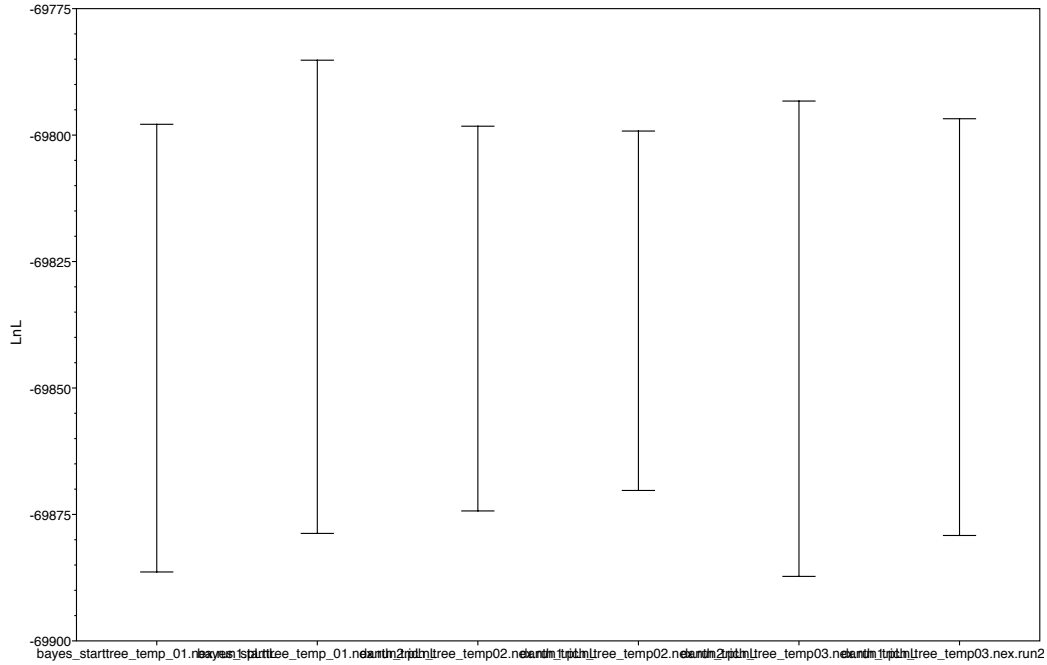
Node number	Node name	p.p.	MRCA of	State (MP)	ML(1)	P(1) mean rjmcmc	age (min95%)	age (max95%)
1	**1**	1.0	Mer_davyi_NPB942 Mer_stereophylla_PM3 Mer_macowanii_NPB1008 Mer_drakensbergensis_PM4	0	0.32580	0.3100	5.85	16.65
2	**2**	1.0	Geo_decora_NPB11 Cap_cincta_NPB1160	0	0.40849	0.3900	16.88	20.73
3	**3**	1.0	Geo_decora_NPB1168 Ryt_quirihuense_MDP338	0	0.44232	0.4220	20.40	22.55
4	**4**	1.0	Pen_praecox_MDP490 Ryt_quirihuense_MDP338	0	0.48264	0.4680	19.75	22.11
5	**5**	1.0	Pen_praecox_MDP490 Pen_pictigluma_mannii_CG267_ITS	0	0.47646	0.4610	11.35	13.37
6	**6**	1.0	Chi_australis_OTA57584_ITS Ryt_quirihuense_MDP338	0	0.44865	0.4300	18.70	21.37
7	**7**	1.0	Pen_praecox_MDP490 Pen_thuarii_HPL5456 Pen_macrocalycina_GAV203	0	0.39789	0.3780	6.11	9.02
8	**8**	1.0	Pen_elegans_CG336 Pen_colorata_CG538 Pen_tortuosa_GAV250 Pen_alticola_CG377 Pen_rigidissima_C	0	0.38574	0.3640	4.10	7.20
9	**8b**	0.99	Pen_colorata_CG538 Pen_clavata_HPL6893 Pen_tortuosa_GAV250 Pen_rigidissima_GAV227	0	0.25092	0.2310	3.41	6.60
10	**8c**	0.91	Pen_alticola_CG377 Pen_colorata_CG538 Pen_clavata_HPL6893 Pen_tortuosa_GAV250	0	0.36442	0.3440	2.32	4.99
11	**9**	1.0	Pen_elegans_CG336 Pen_pictigluma_mannii_CG267_ITS Pen_alticola_CG377 Pen_basutorum_CG44 Pe	0	0.44725	0.4290	6.77	8.82
12	**10**	0.84	Pen_basutorum_CG44 Pen_basutorum_CG44_ITS Pen_andringitrensis_CG595 Pen_pusilla_GAV206 Pen	0	0.47654	0.4680	6.49	8.48
13	**11**	1.0	Pen_pusilla_GAV206 Pen_viscidula_HPL7787 Pen_exserta_CG51 Pen_ampla_GAV197 Pen_aurea_aurea_	0	0.60511	0.6060	5.48	7.11
14	**15**	1.0	Pen_aurea_aurea_HPL6813 Pen_aurea_pilosogluma_CG47	1	0.95370	0.9740	0.55	1.95
15	**16**	0.97	Pen_malouinensis_GAV218_ITS Pen_malouinensis_GAV218 Pen_pungens_CG333	0	0.49679	0.4780	3.76	5.78
16	**17**	0.99	Pen_scandens_CG334 Pen_caulescens_CG376 Pen_curvifolia_TvN52 Pen_acinosa_TvN1 Pen_horrida_Tv	0	0.48198	0.4620	2.96	4.85
17	**20**	0.87	Pen_horrida_TvN20_ITS Pen_malouinensis_GAV218_ITS	0	0.60153	0.5910	0.48	2.60
18	**21**	0.84	Pen_capensis_HPL6825 Pen_pyrophila_GAV229 Pen_argentea_GAV254 Pen_malouinensis_GAV218 Pen_	0	0.49843	0.4850	2.61	4.62
19	**22**	0.95	Pen_argentea_GAV254 Pen_pyrophila_GAV229	0	0.53898	0.5270	2.13	4.15
20	**23**	0.85	Pen_malouinensis_GAV218 Pen_pyrophila_GAV229	0	0.62271	0.6200	1.83	3.72
21	**24**	1.0	Pen_pungens_CG333 Pen_pyrophila_GAV229 Pen_eriostoma_P6	0	0.36150	0.3480	1.39	3.07
22	**25**	1.0	Pen_dentatum_HPL5430 Pen_pictigluma_mannii_CG267_ITS	0	0.51824	0.5150	4.74	6.27
23	**26**	1.0	Pen_dentatum_HPL5430 Pen_velutina_CG389_ITS	0	0.53989	0.5450	3.98	5.65
24	**27**	1.0	Pen_dentatum_HPL5430 Pen_pholiuroides_HPL5402	1	0.78484	0.8010	1.17	2.61
25	**28**	1.0	Pen_rosea_purpurascens_CG378 Pen_horrida_TvN20 Pen_velutina_CG389_ITS Pen_pallescens_GAV216	0	0.38522	0.3700	2.00	3.47
26	**29**	1.0	Pen_trifida_CG577 Pen_velutina_CG389 Pen_triseta_HPL6962 Pen_densifolia_GAV225 Pen_calcicola_ca	0	0.48998	0.4760	4.31	5.82
27	**30**	0.94	Pen_densifolia_GAV225 Pen_pictigluma_mannii_CG267_ITS	0	0.51582	0.5060	3.77	5.15
28	**31**	1.0	Pen_calcicola_calci_CG338 Pen_pictigluma_mannii_CG267_ITS	0	0.60791	0.5980	3.04	4.28
29	**32**	1.0	Pen_calcicola_calci_CG338 Pen_densifolia_GAV225_ITS Pen_ecklonii_HPL6136 Pen_heptamera_CG356	0	0.45645	0.4390	2.35	3.54
30	**35 *new**		Pen_ecklonii_HPL6136 Pen_reflexa_CG324	0	0.55050	0.5410	0.11	0.86
31	**36**	0.86	Pen_cirrhulosa_CG548 Pen_papillosa_GAV209	0	0.20188	0.1880	0.56	1.59
32	**37**	1.0	Pen_chippindalliae_CG96_ITS Pen_reflexa_CG324_ITS Pen_natalensisSA_CG95 Pen_setifolia_CG45 Pen	0	0.70581	0.7000	2.54	3.62
33	**38**	0.96	Pen_glandulosa_HPL6814 Pen_setifolia_CG45 Pen_oreodoxa_CG32	0	0.44453	0.4350	0.63	2.27
34	**40**	1.0	Pen_capillaris_CG322 Pen_veneta_CG576 Pen_airoides_airoides_HPL6971 Pen_galpinii_CG42 Pen_lima_	0	0.62175	0.6200	1.57	2.56
35	**41**	1.0	Pen_capillaris_CG322 Pen_veneta_CG576	0	0.79310	0.8080	0.90	2.02
36	**42**	0.83	Pen_airoides_jugorum_CG81 Pen_airoides_airoides_HPL6971 Pen_galpinii_CG42 Pen_lima_HPL6972 P	0	0.42915	0.4120	1.12	2.18
37	**43**	0.98	Pen_airoides_airoides_HPL6971 Pen_insularis	0	0.22928	0.2310	0.35	1.43
38	**44**	0.93	Pen_airoides_airoides_HPL6971 Pen_insularis Pen_galpinii_CG42 Pen_lima_HPL6972	0	0.62259	0.6180	0.94	1.85
39	**46**	1.0	Pen_aristifolia_CG388 Pen_lima_HPL6972	0	0.30601	0.2880	0.18	0.58
40	**47**	1.0	Pen_borussicaE_HPL7661 Pen_pictigluma_mannii_CG267 Pen_pictigluma_mannii_CG267_ITS	0	0.15126	0.1420	0.64	1.29
41	**49**	1.0	Chi_australis_OTA57584_ITS Chi_defracta_OTA57937 Chi_juncea_OTA57967 Chi_rubra_OTA57960 Ch	0	0.37264	0.3520	13.02	19.34
42	**50**	1.0	Cha_involucratus_dreg_NPB978 Cor_columbiana_ML920 Not_microdon_AMH66_ITS Ten_disticha_NP	0	0.47987	0.4660	15.91	19.54
43	**51**	1.0	Cor_columbiana_ML920 Cor_jubata_ML1515	0	0.40386	0.3820	11.27	16.69
44	**52**	1.0	Cor_bifida_ML1497 Cor_sericantha_ML1128 Cor_boliviensis_ML672 Cor_hieronymi_OM3534 Cor_per	0	0.34245	0.3170	8.91	15.40
45	**53**	0.73	Cor_nitida_ML1434 Cor_jubata_ML1515	0	0.67472	0.6090	3.18	11.35
46	**55**	1.0	Cha_involucratus_dreg_NPB978 Pse_brachyphylla_NPB1669	0	0.49062	0.4790	8.28	11.26
47	**56**	1.0	Not_microdon_AMH66_ITS Ryt_quirihuense_MDP338	0	0.53150	0.5290	14.77	18.46
48	**57**	1.0	Not_microdon_AMH66_ITS Not_microdon_AMH66 Dan_decumbens_MDP312	0	0.55105	0.5490	13.67	17.88
49	**58**	1.0	Ten_disticha_NPB1002 Ten_subulata_HPL7669 Ryt_caespitosum_AMH92 Ryt_australe_AMH145 Ryt_qu	0	0.49776	0.4870	12.31	15.84
50	**59**	0.99	Not_microdon_AMH66_ITS Pli_paradoxa_HPL5638 Pli_rodwayi_MDP415 Pli_urvillei_MC4003	0	0.77164	0.7930	5.31	11.25
51	**60**	1.0	Not_microdon_AMH66_ITS Pli_paradoxa_HPL5638 Aus_splendens_G10872 Aus_toetoe_G5042	0	0.63078	0.6390	9.25	14.19
52	**61**	1.0	Aus_splendens_G10872 Aus_richardii_G3816 Aus_toetoe_G5042 Aus_turbaria_G17358 Aus_fulvida_G50	0	0.14253	0.1300	1.54	4.12
53	**62**	1.0	Cor_pilosa_MDP345 Cor_boliviensis_ITS Cor_hieronymi_ITS Not_microdon_AMH66 Cor_peruvianus_	0	0.46749	0.4390	10.04	15.55
54	**64 *new**		Cor_boliviensis_ITS Not_microdon_AMH66 Cor_jubata_ITS	0	0.65313	0.6120	8.88	14.72
55	**64b**	1.0	Cor_araucana_ITS Cor_jubata_ITS Cor_rudiuscula_ITS	0	0.74489	0.7230	0.79	4.03
56	**65**	0.85	Cor_bifida_ITS Cor_columbiana_ITS Cor_nitida_ITS Cor_sericantha_ITS	0	0.34716	0.3260	5.79	12.87
57	**66**	1.0	Gui_archboldii_JM115 Dan_parryi_CWM813 Dan_compressa_Radford44899 Dan_intermedia_Hermann	0	0.34712	0.3310	6.67	13.89
58	**67**	1.0	Dan_domingensis_AA373 Dan_parryi_CWM813 Dan_spicata_WDT95_30 Dan_unispicata_JTH52406 D	0	0.28558	0.2720	5.61	11.16
59	**68**	0.95	Dan_compressa_Radford44899 Dan_intermedia_Hermannsn Dan_decumbens_MDP312 Dan_chilensis_a	50% (1), 33% eq., 17% (0)	0.35950	0.3500	4.63	10.46
60	**69**	0.97	Dan_alpina_MDP480 Dan_alpina_480_ITS Dan_decumbens_MDP312	0	0.60523	0.6220	1.47	5.35
61	**70**	1.0	Dan_secundiflora_ML1617 Dan_annableae_DMP1833 Dan_filifolia_MJM34 Dan_malacantha_MDP339	0	0.27656	0.2620	2.93	8.13
62	**71**	1.0	Ten_disticha_NPB1002 Ten_subulata_HPL7669	0	0.49802	0.4880	12.00	15.39
63	**86**	1.0	Ryt_alpicolum_AMH102 Ryt_caespitosum_AMH92 Ryt_laeve_Wsn Ryt_pauciflorum_HPL5688 Ryt_bipa	0	0.20609	0.1970	3.20	7.13
64	**87**	1.0	Ryt_alpicolum_AMH102 Ryt_tenuius_AMH70 Ryt_geniculatum_AMH39 Ryt_carphoides_HPL5568 Ryt_	0	0.20152	0.1870	2.57	6.20
65	**90**	1.0	Ryt_buchananii_AMH120 Ryt_maculatum_AMH117 Ryt_telmaticum_AMH151 Ryt_pumilum_NGW667	0	0.48859	0.4580	0.79	2.49
66	**91**	0.87	Ryt_telmaticum_AMH151 Ryt_pumilum_NGW6676 Ryt_thomsonii_AMH118	0	0.87793	0.8090	0.61	1.83
67	**91b**	0.86	Ryt_pumilum_NGW6676 Ryt_thomsonii_AMH118	75% eq., 20% absent, 5% (0)	0.68501	0.6600	0.34	1.33
68	**92**	1.0	Ryt_lechleri_CMB4256 Ryt_violaceum_MDP356 Ryt_australe_AMH145 Ryt_gracile_AMH148 Ryt_setifo	0	0.35570	0.3320	2.28	5.40
69	**93**	1.0	Ryt_australe_AMH145 Ryt_gracile_AMH148 Ryt_setifolium_AMH121	0	0.60011	0.5730	1.77	4.36
70	**94**	1.0	Ryt_australe_AMH145 Ryt_pulchrum_AMH143	0	0.87376	0.8660	1.03	3.08
71	**95**	1.0	Ryt_lechleri_CMB4256 Ryt_violaceum_MDP356	0	0.13420	0.1170	0.96	3.13
72	**96**	0.84	Ryt_gracile_AMH148 Ryt_setifolium_AMH121	0	0.32639	0.3010	1.60	4.23
73	**97**	1.0	Ryt_lechleri_CMB4256 Ryt_pulchrum_AMH143 Ryt_popinensis_AMH94 Ryt_quirihuense_MDP338	0	0.37393	0.3520	2.79	6.26
74	**98**	1.0	Ryt_popinensis_AMH94 Ryt_fulvum_AMH38 Ryt_exiguum_HPL5746 Ryt_quirihuense_MDP338	0	0.45458	0.4260	2.24	5.06
75	**99**	0.98	Ryt_popinensis_AMH94 Ryt_fulvum_AMH38 Ryt_pallidum_HPL5564	0	0.29157	0.2790	2.06	4.65
76	**100**	1.0	Ryt_exiguum_HPL5746 Ryt_vickeryae_MDP422 Ryt_oreoboloides_MWC8877 Ryt_nivicolum_MDP419	0	0.67944	0.6440	1.70	4.14
77	**101*new**		Ryt_exiguum_HPL5746 Ryt_oreoboloides_MWC8877	0	0.71381	0.6860	1.47	3.37
78	**103**	0.99	Ryt_merum_AMH125 Ryt_caespitosum_AMH25 Ryt_quirihuense_MDP338	0	0.17968	0.1640	1.42	3.31

Grey shading: ancestral state = '0'; yellow shading: ancestral state = '1'; no shading: ancestral state = ambiguous.

Figure S1 A-C. Likelihood values for Bayesian phylogeny reconstruction.



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LnL
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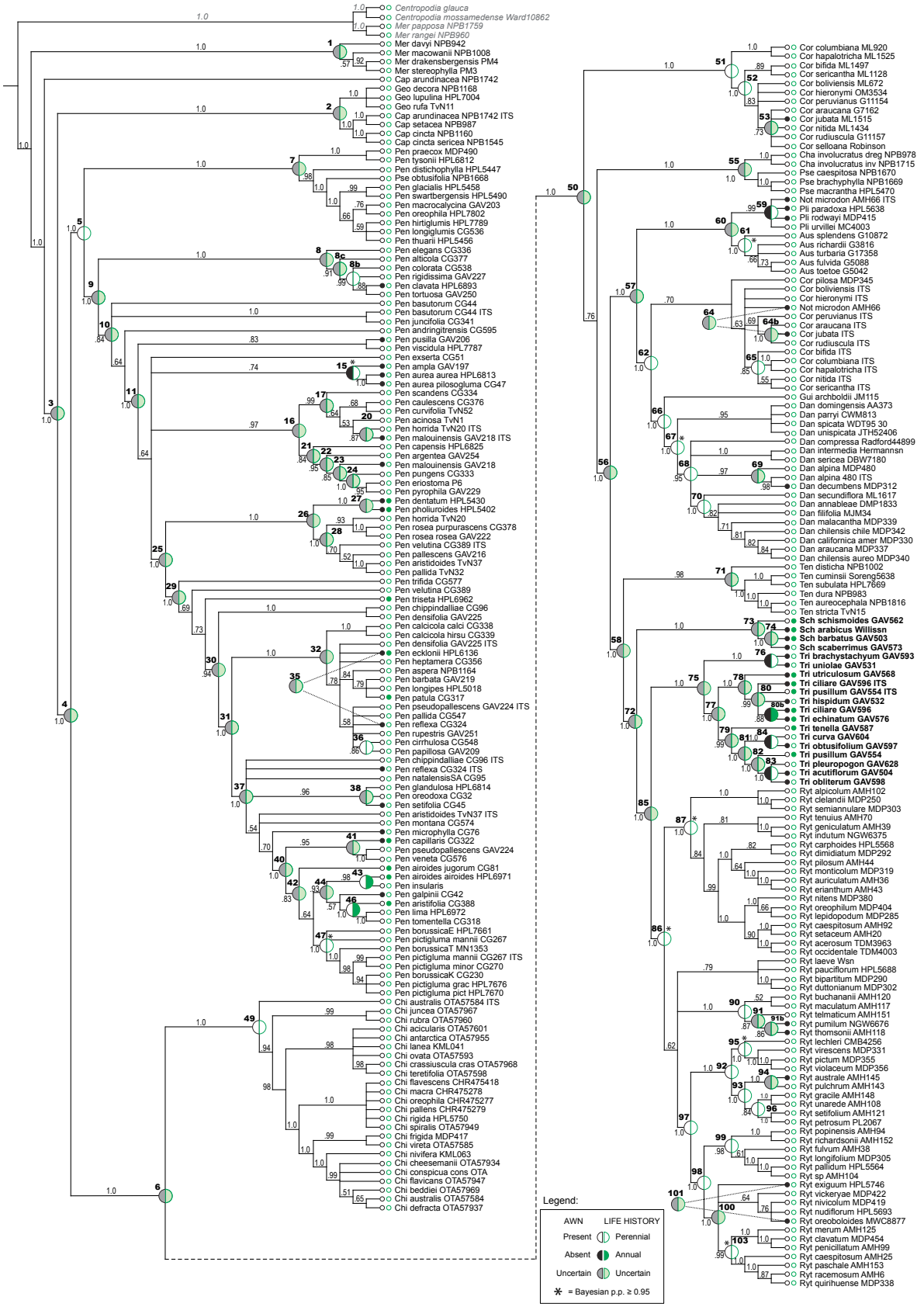
random_startree_temp02.nex.run1
random_startree_temp02.nex.run2
random_startree_temp03.nex.run1
random_startree_temp03.nex.run2

Figure S2. A randomly selected phylogram from optimal posterior sample of Bayesian trees to show branch length differences among and within clades.

Figure S3. Ancestral state reconstructions assuming correlated evolution between awns and life history.



Concluding remarks

In this thesis I argue that shifts in generic concepts drive changes in overall genus sizes and that the current trend toward recognising larger genera is a result of a return to study on a broad scale, rather than incorporation of molecular data (Chapter 1). I demonstrate that a phylogenetic hypothesis of *Rytidosperma* and allied genera, based on plastid data, has significant support from morphological, ecological and distribution data and can therefore act as a guide for revision of the generic limits among the ca. 100 species concerned (Chapter 2). I characterise variation in diaspore characters in the Danthonioideae as constituting two extremes of a burial syndrome and show that lineages where this burial syndrome is optimised toward active burial, driven by hygroscopic movement of the awn, are in general more diverse and persistent than lineages that have lost their awn (Chapter 3).

These theses raise a suite of further questions. What, for example, were the detailed ecological and geographical drivers of the evolution of *Rytidosperma* in Australasia and South America? The genus contains lowland, alpine and montane species as well as species (Plates 1 and 2). Some species are geographically and ecologically widespread and others have a narrow range in one other, or both, of these respects. The data analysed here suggest multiple ecological shifts at the level of sister species, in turn suggesting that ecological divergence could have been a strong evolutionary force in this group. Resolution of this question would require a hypothesis of phylogeny that is more detailed and densely sampled toward the tips, including consideration of patterns contained in the nuclear genome. Experimental manipulation of the observed niches of closely related species would shed further light on the ecological distinctiveness of extant species and the possible role of ecological divergence in their evolution.

How old are the individual extant species? Several species are used agriculturally in Australia and have been shipped between continents for centuries. Some species that have been introduced beyond their native range have become widespread weeds (e.g. *Danthonia decumbens* in Australia, *Schismus barbatus* and *Rytidosperma penicillatum* in North America) providing novel opportunities for genetic exchange. What might the origin(s) of *R. paschale* (Plate 8E) on Easter Island and *R. quirihuense* (Plate 5H) on the coast of Chile be? These species are the only lowland members of South American *Rytidosperma*. Both molecular and morphological data suggest that they are more closely related to a group of lowland species from Australia, than to their Andean counterparts. Resolution of the age and geographical patterns associated with the origin of these species could cast new light on our understanding of 'natural' diversity and would again require analysis of molecular data from the plastid and the nuclear genome, sampled at the population level, together with analysis of historical and archaeological records.

Experimental confirmation of the function of the two extremes of the 'burial syndrome' on different soil types would strengthened the thesis put forward here and would provide an avenue for furthering our understanding of the ecology of diaspore (seed) burial. What are the circumstances under which active burial is a real advantage and the circumstances under which it is redundant and can be lost? A starting point for addressing this question would be to extend the macroevolutionary analyses of this trait to other groups, both in Poaceae and beyond, to search for correlates of the presence and absence of awns more broadly.

Finally, I wonder whether there will ever be true consensus among (plant) systematists regarding how best to delimit genera. If not, and the major dichotomy identified here rings alarm bells, what are the consequences for comparative approaches to evolution, ecology and conservation studies? Further studies of the evolutionary nature and history of higher taxa might provide a starting point to objective delimitation of genera that constitute comparable units in an evolutionary sense.

Curriculum vitae

Surname:	HUMPHREYS
First names:	Aelys Muriel
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Nationality:	British

Education

Secondary schools:	Skolhagenskolan, Täby, Sweden, 1994, *Slutbetyg Grundskolan* Åva Gymnasium, Täby, Sweden, 1997, *Slutbetyg Matematiskt Naturvetenskapligt Program*
Undergraduate universities:	**Bachelor of Science, Biological Sciences, with Plant Science Honours**, University of Edinburgh, U.K. (1998-2002) **Erasmus exchange** semester, 20 ECT points, Uppsala Universitet, Sweden (2000)
Postgraduate university:	**Master of Research** in Biosystematics, Imperial College London, U.K. (2003-2004)
Master of Research theses:	**1.** Untangling the species complex *Trema micrantha* (L.) Blume (Celtidaceae) using molecular markers and leaf trichome characters **2.** Evolutionary studies in the soft slipper fungus, *Crepidotus* (Basidiomycota: Agaricales) **3.** Using supermatrix and supertree approaches to infer the evolution of asplenioid ferns (*Asplenium*, Aspleniaceae)
Ph.D. thesis:	Generic delimitation and macroevolutionary studies in Danthonioideae (Poaceae), with emphasis on the wallaby grasses, *Rytidosperma* Steud. s.l.

Employed as a Ph.D. student at the University of Zurich since September 2005

Publications during Ph.D. studies

Humphreys, A.M., Wüest, R., Linder, H.P. (in preparation) Frost tolerance of Southern Hemisphere grasses (Danthonioideae: Poaceae). *New Zealand Journal of Botany*.

Pirie, M.D., **Humphreys, A.M.,** Galley, C., Antonelli, A., Linder, H.P. (in preparation). Reconstructing the biogeographic history of Danthonioideae (Poaceae).

Humphreys, A.M., Antonelli, A., Pirie, M.D., Linder, H.P. (submitted) Ecology and evolution of the diaspore 'burial syndrome'. *Evolution*.

Antonelli, A., **Humphreys, A.M.,** Lee, W.G., Linder, H.P. (submitted) New Zealand grasses adapted to the absence of mammals. *Current Biology*.

Linder, H. P., M. Baeza, N. P. Barker, C. Galley, **A. M. Humphreys,** K. Lloyd, D. Orlovich, M. D. Pirie, B. K. Simon, N. Walsh, and G. A. Verboom. 2010. A Classification of the Danthonioideae (Poaceae). *Annals of the Missouri Botanic Garden.* Accepted for publication.

Humphreys, A.M., Pirie, M.D., Linder, H.P. 2010. A plastid tree can bring order to the chaotic generic taxonomy of Rytidosperma Steud. s.l. (Poaceae). *Mol. Phylogenet. Evol.* 55:911-928

Humphreys, A.M., Linder, H.P. 2009. Concept versus data in delimitation of plant genera. *Taxon* 58, 1054-1074.

Pirie, M.D., **Humphreys, A.M.,** Barker, N.P., Linder, H.P., 2009. Reticulation, Data Combination, and Inferring Evolutionary History: An Example from Danthonioideae (Poaceae). *Systematic Biology* 58, 612-628.

Pirie, M.D., **Humphreys, A.M.,** Galley, C., Barker, N.P., Verboom, G.A., Orlovich, D., Draffin, S.J., Lloyd, K., Baeza, C.M., Negritto, M., Ruiz, E., Sanchez, J.H.C., Reimer, E., Linder, H.P., 2008. A novel supermatrix approach improves resolution of phylogenetic relationships in a comprehensive sample of danthonioid grasses. *Mol. Phylogenet. Evol.* 48, 1106-1119.

Professional activities during Ph.D. studies

Seminar organisation:	**Field Trip Slideshows**, departmental seminar series at the Institute of Systematic Botany and Botanic Gardens, University of Zurich (2006-2009) **PSC Symposium** 'Plants and People Mutual Dependence in the 21st Century', PhD Symposium of the Zurich—Basel Plant Science Center (PSC) (2008). One of six organisers.
Internal review of articles for:	Antonelli, A. (*BMC Biology*) Bouchenak-Khelladi, Y. (*Global Change Biology*) Gehrke, B. (*Proceedings of the Royal Society Series B*) Hock, Z. (*American Journal of Botany*) Kessler, M. (manuscript) Pirie, M. (*Journal of Biogeography*) Rutishauser, R. (abstract in English for *Vierteljahrsschrift der Naturforschenden Gesellschaft in Zürich*) Schneller, J. (*American Journal of Botany; Plant Systematics and Evolution*) Urmi, E. (course instructions) Van der Niet, T. and Gehrke, B. (*Journal of East African Natural History*) Weckerle, C. (*Journal of Ethnopharmacology*)
Teaching assistance:	**Biology/Life sciences** undergraduate courses BIO113, BIO123 and MAT182 (2009-2010) **Ethnobotanik und Ethnomedizin**, Zertifikatstudiengang, University of Zurich (2008)
Public outreach:	Guided tour, Botanic Gardens Zurich, 'Frost tolerance of Southern Hemisphere grasses' (in German) (2010) Guide at 'Tree of Life' exhibition, Zurich Central Station (2009) Fruit sales at the 'Obstsortenmarkt', Botanic Gardens Zurich (2007 & 2009)

Employment during Ph.D. studies

Electronic learning platform development for undergraduate/Master's level courses on 'Scientific Writing' and 'Responsible Conduct in Science', PSC Center, ETH Zurich (2009). My responsibilities during this 5-month 50% employment included developing guidelines for different text types (e.g. research article and review article); composing learning activities to aid developing skills required for scientific writing; uploading and editing content of both learning platforms (Leaning Management System and HTML).